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ORIGINAL PAPER

Younger Dryas and early Holocene subsistence in the northern Great Basin: multiproxy analysis of coprolites from the Paisley Caves, Oregon, USA

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Abstract

Younger Dryas and early Holocene Western Stemmed Tradition occupants of the northern Great Basin appear to have practiced a broad-based subsistence strategy including the consumption of a wide variety of small animal and plant resources. However, much of our evidence for human diet and land use during this period comes from dry cave and rockshelter sites where it can be challenging to distinguish plant and small animal remains deposited as a result of human versus nonhuman activity. This study presents new direct evidence for Younger Dryas and early Holocene human diet in the northern Great Basin through multiproxy analysis of nine human coprolites from the Paisley Caves, Oregon, USA. The evidence indicates that Western Stemmed Tradition occupants consumed plants, small mammals, fish, and insects, including direct evidence for consumption of whole rodents and several types of beetle. Occupation of the caves occurred during the summer and fall by individuals foraging on wetland, sagebrush grassland, and riparian ecological landscapes suggesting geographical and seasonal variability in land-use patterns during the Younger Dryas and early Holocene periods. This research suggests that Western Stemmed Tradition settlement patterns were seasonally centered on productive valley bottom lakes and wetlands but also included forays to a variety of ecological landscapes. The results highlight the importance of plant and small animal resources in the human diet during the terminal Pleistocene settlement of North America and contribute to debates about the process of the peopling of the Americas.

Keywords Western Stemmed Tradition · Hunter-gatherer diet · Younger Dryas · Great Basin · Coprolite

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Introduction

The Great Basin of North America offers informative case studies of regional hunter-gatherer subsistence and land-use adaptations during the first several millennia of human occupation of the Americas. Great Basin sites dating to the Younger Dryas (YD) cold period (12,900–11,700 cal BP) and early Holocene (EH) warm period (11,700–8900 cal BP) typically contain Western Stemmed Tradition (WST) projectile points and related technology (Beck and Jones 1997; Jenkins et al. 2012; Smith and Barker 2017; Smith et al. 2020). Preserved organic remains at a few widely separated WST sites in the Great Basin suggest a perplexing array of settlement–subsistence scenarios. YD/EH occupants may have had a broad-based subsistence strategy including a wide variety of small animal and plant resources centered on productive valley bottom lacustrine settings and surrounding

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grasslands (Beck and Jones 1997; Bedwell 1973; Madsen 2007; Smith and Barker 2017; Hockett 2015; Hockett et al. 2017; Jenkins et al. 2016; Smith and Barker 2017), or, they may have maintained much higher mobility and a more restricted diet focused on large-bodied mammals (Elston and Zeanah 2002; Elston et al. 2014; Jones et al. 2003).

Addressing the debate about the nature of WST subsistence and land-use patterns has been hampered by the paucity of direct evidence of human diets from this period (Smith and Barker 2017). The most direct method for understanding past human dietary decisions is through the analysis of coprolites (Battillo 2019; Bryant 1974b; Callen 1963; Riley 2008, 2010). Here we present a multiproxy analysis of pollen, phytolith, macrobotanical, faunal, and insect remains from nine YD/EH human coprolites recovered at the Paisley Caves in south central Oregon (Fig. 1), providing new evidence for WST human diets. This evidence is evaluated within the broader record of YD/EH subsistence at the Paisley Caves and used to test WST subsistence and land-use models. The results provide support for a broad-based subsistence strategy employed during summer/fall occupations of the caves during the WST period. This research highlights the importance of plant and small animal resources in the human diet during the terminal Pleistocene settlement of North America. The results of this study inform broader debates about specialized large mammal versus generalized and regionally variable subsistence strategies during this time.

YD/EH archaeology of the northern Great Basin

WST occupations at the Paisley Caves have been dated as early as 13,000 cal BP and offer a robust data set to evaluate early subsistence–settlement systems in the northern Great Basin (Jenkins et al. 2012, 2013). WST toolkits in the region are typically made from locally available high-quality toolstone—obsidian, in particular—that was often transported across hundreds of kilometers suggesting high mobility (Jones et al. 2003; Smith 2010). Technology was flexible and maintainable, characteristics typically associated with high mobility (Elston and Zeanah 2002; Elston et al. 2014). WST lithic assemblages lack heavy ground stone milling equipment and are instead dominated by formally flaked tools (bifacial and unifacial) and large projectile points presumed to function as tools to hunt and process large-bodied mammals (Elston and Zeanah 2002). These attributes suggest highly mobile land-use strategies and an overall reliance on a narrow set of high-ranked food resources (Beck and Jones 1997; Elston et al. 2014; Goebel et al. 2011). However, WST cave and rockshelter sites containing stratified, well-dated, and well-preserved YD/EH deposits provide evidence for a diverse diet of large-, medium-, and small-bodied mammals; birds; fishes; insects; seeds; and roots (Aikens et al. 2011; Grayson 1988; Hockett and Jenkins 2013; Jenkins et al. 2013, 2016; Kennedy and Smith 2016; Smith and Barker 2017).

WST sites in the northern Great Basin are typically associated with valley bottom wetland and riparian zones (Smith and Barker 2017). There is strong evidence for textile

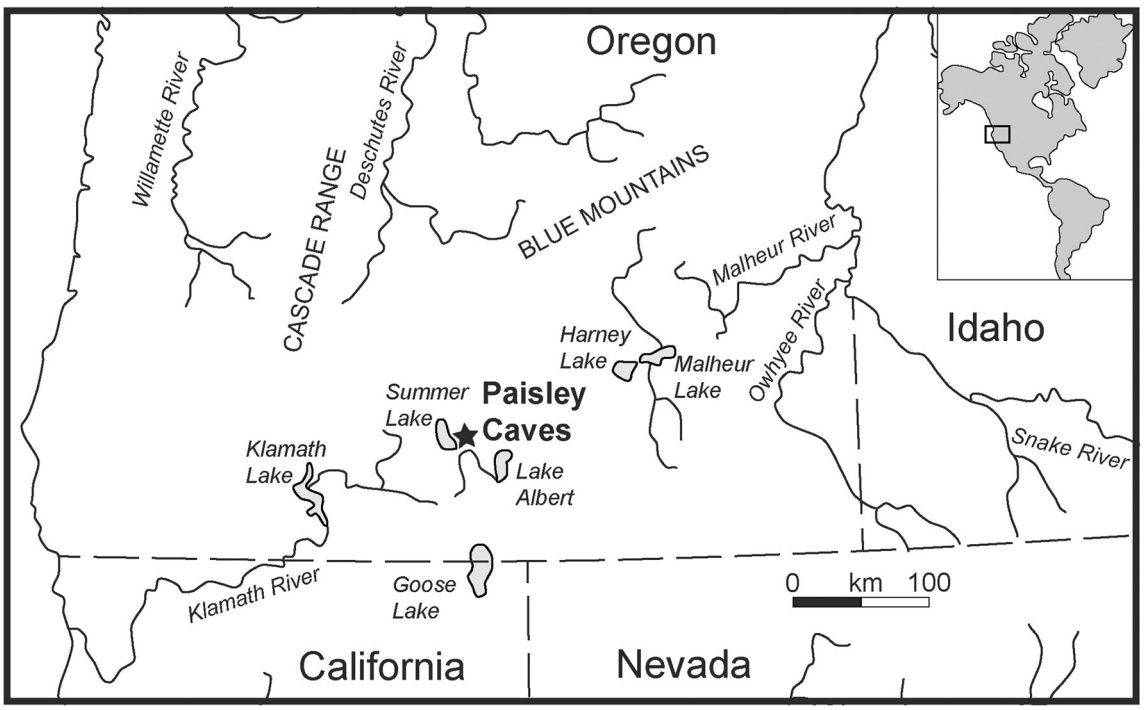

Fig. 1 Map showing the location of the Paisley Caves in southcentral Oregon

production requiring raw materials from wetland and sagebrush steppe ecological zones (e.g., tule and sagebrush bark) and investment in production (Smith and Barker 2017). These characteristics suggest WST occupants of the region lived in longer-term residential camps near wetlands for part or most of the year (Elston et al. 2014; Madsen 2007; Smith and Barker 2017). However, WST sites are also found in mid-elevation and upland locations, including upland rock art sites in well-known root grounds (Middleton et al. 2014; Ricks and Cannon 1993; Smith and Barker 2017). The density of archaeological deposits at some EH sites suggests they may have functioned as residential camps; however, the paucity of storage or structural features at most sites indicates they were most commonly ephemeral occupations (Smith and Barker 2017). These characteristics suggest that WST hunter-gatherers in the northern Great Basin were not always tethered to low-elevation wetland habitats and may indicate a wide-ranging seasonally variable settlement–subsistence strategy (Aikens et al. 2011, p. 71; Jones et al. 2003; Smith 2010).

The archaeological record of the northern Great Basin largely mirrors that of the broader Great Basin. WST lithic toolkits across the Great Basin provide evidence for highly mobile land-use strategies (Graf 2001; Jones et al. 2003, 2012; Smith 2011). Blood protein residue analysis of a WST projectile from western Utah and two handstones from Paisley Caves provide evidence for hunting of Proboscidean and Equus prey (Duke 2015; Jenkins et al. 2013). However, well-preserved deposits from YD/EH occupations at cave and rockshelter sites like Smith Creek Cave (Bryan 1980), Bonneville Estates Rockshelter (Hockett 2007, 2015; Rhode and Louderback 2007), Hogup Cave (Aikens 1970; Fry 1970, 1976; Harper and Alder 1970; Herzog and Lawlor 2016), and Danger Cave (Fry 1970, 1976, 1978; Grayson 1988; Jennings 1957; Parmalee 1988; Rhode and Louderback 2007; Rhode et al. 2006) contain plant, insect, large animal, and small animal remains suggesting a broad-based subsistence strategy, although these often are not unequivocally linked to human occupation (e.g., Goebel et al. 2011; Grayson 1988; Rhode and Louderback 2007). Despite the growing body of data supporting broad-based diets and seasonally variable land use during the WST period, we have very little direct dietary evidence to inform current debates. Coprolite studies in the Great Basin provide direct evidence for WST subsistence; however, there are a limited number of sites with coprolites from this period (Cummings et al. 2007; Fry 1970, 1976; Napton 1997).

Determining the nature of terminal Pleistocene subsistence–settlement strategies in the Great Basin is important because it links to broader debates about the process of initial human settlement of North America. The first widely distributed archaeological complex in North America was long thought to be the Clovis complex, primarily identified by the presence of lanceolate-shaped fluted projectile points associated with radiocarbon dates ca. 13,250–12,700 cal BP (Bradley et al. 2010; Collins 1999; Waters and Stafford Jr 2007; Waters et al. 2011). Clovis assemblages are often associated with now-extinct Pleistocene large mammal remains, especially mammoth (*Mammuthus* sp.), and are thought to represent highly mobile large mammal hunters moving into previously unoccupied parts of North America at the end of the Pleistocene (Haynes Jr. 1966; Haynes 2002; Kelly and Todd 1988; Surovell and Waguespack 2008; Waguespack and Surovell 2003).

Fluted points are found in the Great Basin; however, they have not been found in well-dated contexts. The few radiocarbon dates associated with fluted technology in the Great Basin indicate an age range of 13,100–8400 cal BP (Beck and Jones 2013; Goebel and Keene 2014; Smith et al. 2020). Great Basin fluted points exhibit considerable variability in form suggesting they are younger than those east of the Rocky Mountain divide (Beck and Jones 1997, 2013; Davis et al. 2012). Sites like the Paisley Caves, Cooper's Ferry, and the Debra L. Friedkin site present evidence that WST assemblages in western North America are co-eval with and possibly even older than Clovis assemblages (Davis et al. 2019; Jenkins et al. 2012; Waters et al. 2018). This evidence suggests that the initial occupation of western North America may not be related to the widespread Clovis archaeological complex—instead, the WST may represent initial settlement by hunter-gatherers linked to Pacific coastal-adapted settlers (Davis et al. 2012; Madsen et al. 2015). Understanding WST subsistence–settlement systems, then, is crucial for understanding the process of the initial settlement of North America.

Paisley Caves site background and environmental context

The YD was a period of rapid climate fluctuation in North America (Rasmussen et al. 2014). During this time, temperatures cooled, effective moisture increased in the northern Great Basin, and lakes and wetlands covered many valley bottoms including near the Paisley Caves in the Chewaucan Basin (Grayson 2011; Jenkins et al. 2016). Paleoenvironmental studies at the Paisley Caves indicate sagebrush steppe vegetation on the surrounding landscape with possible eastward expansion of forested areas from the Cascade Mountains into the grasslands of the northern Great Basin (Beck et al. 2018; Saban and Jenkins 2013; Saban 2015). The EH saw a shift toward a warmer, more arid climate in the northern Great Basin, with the summer insolation maximum peaking at 11,000 cal BP. During this time, many valley bottom lakes shrank, forming extensive wetland marshes that were productive habitats for fish, waterfowl, and mammals (Grayson 2011; Minckley et al. 2004). Paleoenvironmental research at the Paisley Caves supports a transition to more xeric taxa with

subalpine conifer and marsh communities nearby (Beck et al. 2018; Saban and Jenkins 2013; Saban 2015).

The Paisley Caves are one of the most extensively studied sites in the northern Great Basin, with well-dated cultural sequences in three caves (1, 2, 5) spanning the terminal Pleistocene through historic period (Jenkins et al. 2013; Jenkins et al. 2016). This study focuses on the WST record from caves 2 and 5. Five primary lithostratigraphic units (LU) have been defined in caves 2 and 5 representing approximately 16,000 years of eolian, volcanic, biogenic, and anthropogenic deposition (Jenkins 2007; Jenkins et al. 2012; Jenkins et al. 2016) (Fig. 2). WST material in cave 5 is concentrated in LU 2, consisting of loose to indurated organic sandy deposits associated with dates spanning the latter part of the Bølling-Allerød through the EH (Jenkins et al. 2012, Jenkins et al. 2016). WST material in cave 2 is most commonly associated with the distinctive "botanical lens" cultural horizon ephemerally expressed at the base of LU 3 and its contact with underlying LU 2 (Jenkins et al. 2016). The botanical lens is marked by matted sagebrush (*Artemisia* sp.) twigs and shredded bark, 5–8 cm thick where undisturbed, deposited between 12,320 and 11,960 cal BP (Jenkins et al. 2016). The botanical lens contains remarkably well-preserved evidence of human occupation including hearth features; pronghorn (*Antilocapra americana*), white-tailed jackrabbit (*Lepus townsendii*), and marmot (*Marmota* sp.) hair, hide, and bone fragments; fish, waterfowl, greater sage grouse (*Centrocerus urophasianus*) and insect remains including Mormon cricket (*Anabrus simplex*), bed bug (*Cimex* sp.), and spinose ear tick (*Otobius megnini*) (Adams and Jenkins 2017; Adams and Jenkins 2020; Hockett et al. 2017). Numerous organic artifacts include cordage, rope, basketry, and wood tools. Lithic assemblages from caves 2 and 5 include WST projectile points, bifaces, scrapers, flake knives, edge-modified flakes, cores, and grooved scoria abraders (Jenkins et al. 2012, Jenkins et al. 2016). Human activity at the Paisley Caves during the YD/EH is currently interpreted to represent short-term seasonal occupations when local resources were most abundant, for example, during spring and late summer/fall (Jenkins et al. 2016; Kennedy 2018).

Previous research at the Paisley Caves has characterized YD/EH subsistence using plant and animal remains recovered in dry- or wet-screened sediments from cultural deposits in the caves (Hockett et al. 2017; Kennedy 2018). These studies provide important evidence that people with WST toolkits occupying the caves consumed small animal, plant, and insect foods. However, the caves were also inhabited by many non-human species over the millennia, and it can be challenging to distinguish organic materials resulting from human subsistence from those that are the result of noncultural processes such as animal nesting and carnivore activity (Andrews 1990; Sauqué et al. 2018). Excavations at the Paisley Caves have produced a substantial assemblage of human coprolites from YD/EH contexts. Coprolites commonly contain preserved plant and animal macrofossil and microfossil remains that can be used to reconstruct dietary choices made by the individual (Callen and Martin 1969; Fry 1976; Reinhard and Bryant Jr 2008). This high-resolution record of human diet is well-suited to addressing the relative importance of small animal and plant food resources and the nature of WST

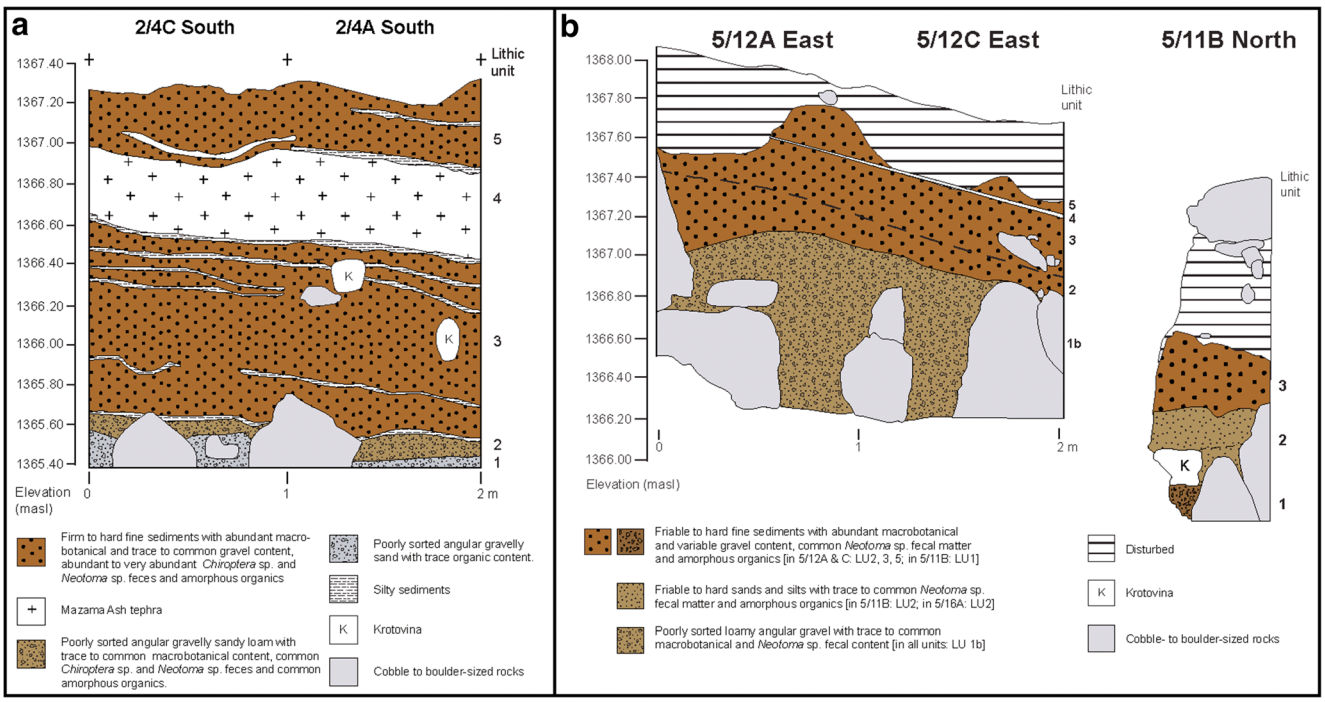

Fig. 2 Stratigraphic profiles showing lithic units defined in Paisley Cave 2 (**a**) and Paisley Cave 5 (**b**). Images redrawn from Jenkins et al. 2012

seasonal land-use patterns as expressed at the Paisley Caves. It provides important information for investigating the broader nature of YD/EH subsistence–settlement systems in the northern Great Basin.

Here, we present a new study of coprolites from Paisley Caves combining multiproxy (plant and animal macrofossil, pollen, and phytolith) analyses of nine probable human coprolites recovered from YD/EH contexts in Paisley Cave 2 and 5. Multiproxy coprolite studies are critical because they provide multiple lines of direct evidence for human dietary choices, and offer the possibility of constraining seasonal models of occupation (Milner 1999; Monks 1981; Shillito et al. 2020a).

Materials and methods

Coprolite sampling and morphological description

Each coprolite was photographed and described following Jouy-Avantin et al. (2003). Coprolites were initially chosen for this study based on physical characteristics suggesting human origin (following Bryant 1974b). These determinations were made with the caveat that physical characteristics alone cannot always accurately identify the species of animal that deposited the coprolite (Bryant 1974b; Chame 2003; Reinhard and Bryant Jr 2008; Shillito et al. 2011; Shillito et al. 2020a). The sampling process is summarized in Fig. 3 and the coprolites are shown in Fig. 4. Coprolites were cut along the long axis using a sterile disposable scalpel and one half of each was employed in this study. The other half has been retained in the sample archive. Collecting a subsample representing the entire length of the coprolite is preferred because macro- and microfossils can be unequally distributed along the length of a coprolite as a by-product of consuming different meals (Beck et al. 2019; Martin and Sharrock 1964). The exception to this methodology occurred with samples 57, 195, and 215, which consisted of already-fragmented coprolite material; for these three samples, a discrete fragment was collected for our analysis to preserve as much intact material as possible for future research.

For most subsamples, the exterior layer of coprolite material was scraped off using a sterile scalpel to remove potential contaminants, thereby creating an "interior" coprolite sample. The interior material was processed for pollen, phytolith, and plant and animal macrofossils as described in the following sections. However, it was not possible to secure an interior sample when the coprolite was very small, fragmented, or had a very friable consistency. In these cases, the entire subsample (interior and exterior) was processed for this analysis. Coprolite subsamples were soaked for 24–96 h in a 0.5% sodium phosphate solution until rehydrated and softened (Callen and Cameron 1960). The color of the solution (using a Munsell color chart) and opacity was recorded after the coprolites were rehydrated (Bryant 1974b). The coprolite samples are summarized in Table 1.

Radiocarbon dating

Macrofossils were recovered from coprolites 55, 98, and 242 following the methods described below, then dried,

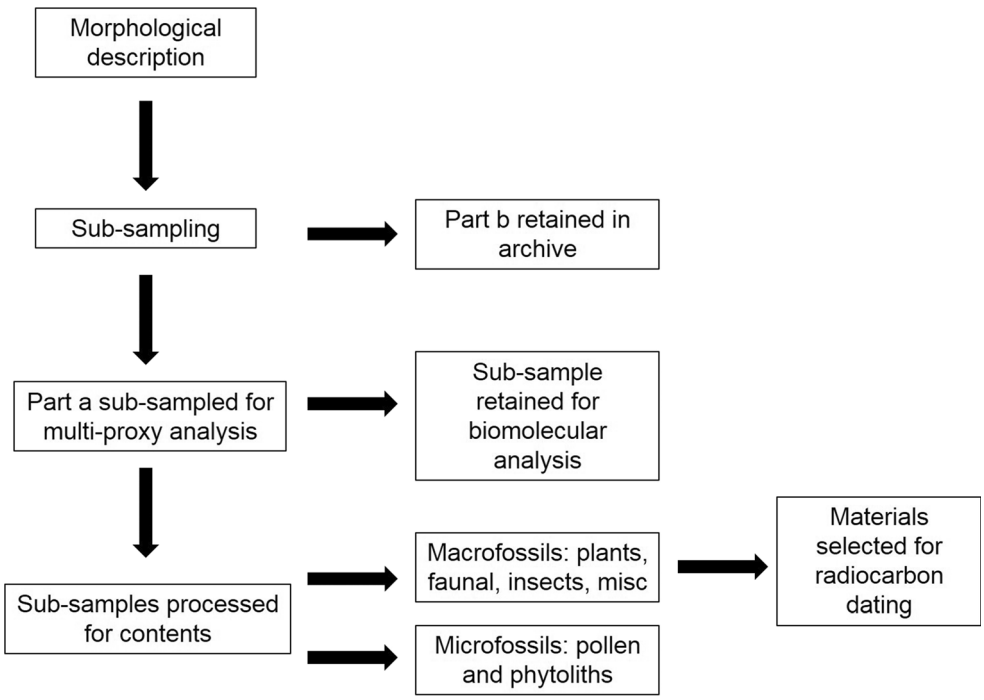

Fig. 3 Summary of coprolite sampling methodology

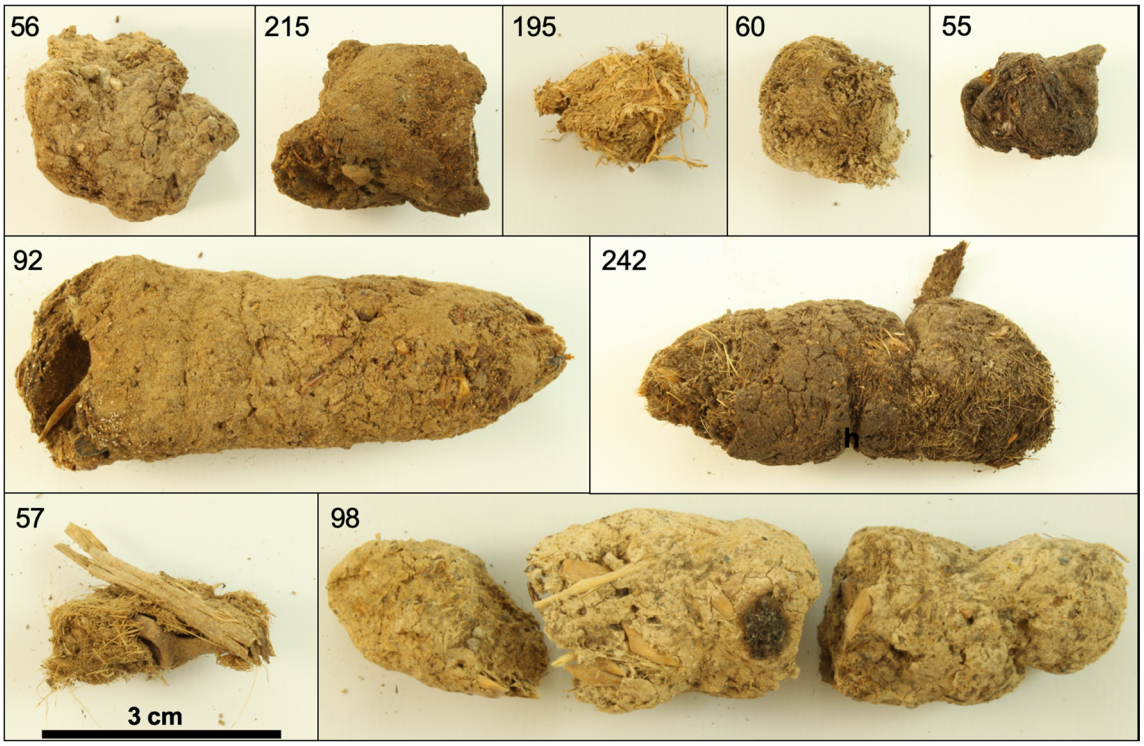

Fig. 4 Images of the nine Paisley Caves coprolites prior to collecting the subsamples processed for this study. Sample information in Table 1

weighed, and submitted for radiocarbon analysis. Samples consisted of combined plant material (e.g., plant fiber, charcoal fragments); this was deemed appropriate because coprolites represent a tightly constrained context and there is little chance for intrusive macroscopic organic material that might contaminate radiocarbon samples. Samples were sent to the Oxford Radiocarbon Accelerator Unit for AMS analysis.

Analysis of contents

Between two and four *Lycopodium clavatum* marker spore tablets (batch number 3862; 9666 spores per tablet) were added to each rehydrated coprolite sample to enable pollen concentration calculation (Bryant Jr and Hall 1993; Davis 1966; Stockmarr 1971). The rehydrated coprolite material was gently disaggregated, screened through 250-μm mesh sieve, then finished with a spray of ethanol to break surface tension and release any microfossils trapped in the screen. The > 250-μm material remaining on the screen was stored in distilled water at 4 °C for macrofossil analysis. The < 250-μm material was treated with a 5% solution of sodium hexametaphosphate to disaggregate the sample and remove any clay particles. The liquefied < 250-μm material was then split evenly into phytolith and pollen subsamples.

Plant and animal macrofossil analysis

Macrofossil remains were suspended in a glass dish containing distilled water and examined with the aid of a stereomicroscope under × 20 to × 40 magnification to separate different coprolite components (e.g., stone, insect, plant fiber, seeds). The resulting groups of material were dried in an oven at 100 °C, then weighed. Raw weight data is presented as well as percent weight calculated by dividing the weight of individual components by the total weight of all < 250-μm macrofossil material. Percent weight of material per sample is used to make the data more comparable between coprolites (Faulkner 1991; Fry 1970). Seeds, bone, and insect remains were counted and are presented as the total number of fragments (NISP) and estimated minimum number of individual (MNI) specimens (Grayson 1984). For seeds, the MNI estimate is based on the number of fragments representing more than 50% of a seed as well as the presence/absence of distinctive features (e.g., hilum). Plant macrofossil analysis primarily focused on seeds as these can often be identified with high taxonomic resolution (Birks 2007). Seed identifications were made using reference material at Newcastle University as well as seed reference material obtained from the USDA National Clonal Germplasm Repository (https://npgsweb.ars-grin.gov/gringlobal/search.aspx) and online resources specific to the Great Basin (https://nhmu.utah.edu/native-plants).

Table 1 Summary of sample morphological descriptions and data. Samples are listed from oldest to youngest

Sample	Age[a]	Paisley catalog number	Weight (g)[b]	Rehydrated color and translucency	Maximum length × width × thickness (mm)	Volume	Taphonomic modifications	Inclusions	Hardness	Previous research	Provenience information
57	12,820–12,665 cal BP (10,833 ± 59; UGAMS-A26418)	1961-PC-2/7C-18-50	0.81 (E)	Dark yellowish brown (10 YR 4/6), translucent	26.8 × 10.96 × 10.88	Unknown	Absent	Bone, plant	Friable	Sample B-3 in Taylor et al. (2019)	Cave 2, unit 7, quad C, LU 2. Elevation 1365.75 masl. Coprolite directly dated
195	12,629–12,416 cal BP[c] (10,050 ± 50; Beta-213423), (10,965 ± 50; OxA-16376)	1294-PC-5/6B-40-6	0.32 (E)	Dark yellowish brown (10 YR 4/6), translucent	17.3 × 15.28 × 9.49	Unknown	Fragment too small to determine	Plant, round stone	Friable	Sample 1294-PC-5/6B-40 with *Homo sapiens* haplogroup B2 and *Canis lupus/familiaris* mtDNA (Gilbert et al. 2008)	Cave 5, unit 6, quad B, LU 1a. Elevation 1366.40–1366.35 masl. Coprolite directly dated
98	12,515–12,087 cal BP (see Table 2)	1896-PC-2/6D-51-12	5.24 (I)	Very dark brown (7.5 YR 2.5/3), semi-opaque	94.56 × 62.72 × 57.34	Cylindrical[d]	Vacuole	Round stone, bone, hair, plant	Hard		Cave 2, unit 6, quad D, LU 3. Elevation 1365.75 masl. Coprolite directly dated
60	~ 12,200 cal BP	1961-PC-2/7D-17-138	0.34 (E)	Dark brown (10 YR 3/3), semi-opaque	17.03 × 16.47 × 12.51	Unknown	Fragment too small to determine	Hair, bone, charcoal	Friable		Cave 2, unit 7, quad D, LU 3. Elevation 1365.8. Radiocarbon date on cut-artiodactyl bone from the same 5-cm level in quad D 10,350 ± 40 (BETA-429640)
55	12,376–11,767 cal BP (see Table 2)	1961-PC-2/7C-16-136	0.41 (E)	Black (7.5 YR 2.5/1), opaque	16.75 × 14.13 × 13.22	Unknown	Absent	Charcoal, insect, bone, hair	Hard	Sample B-7 in Taylor et al. (2019)	Cave 2, unit 7, quad C, LU 3 Elevation 1365.85. Coprolite directly dated
56	12,065–11,766 cal BP (10,207 ± 32; UGAMS--A26420)	1961-PC-2/7C-16-138	2.45 (E)	Very dark brown (7.5 YR 2.5/2), semi-opaque	23.9 × 26.65 × 17.35	Unknown	Absent	Plant, bone	Hard	Sample B-9 in Taylor et al. (2019)	Cave 2, unit 7, quad C, LU 3. Elevation 1365.85. Coprolite directly dated
242	11,196–10,823 cal BP (see Table 2)	1895-PC-5/16A-21-1	2.7 (I)	Very dark brown (7.5 YR 2.5/3), opaque	48.93 × 20.34 × 17.13	Cylindrical[d]	Fissure	Bone, hair	Hard		Cave 5, unit 16, quad A, LU 2. Elevation 1366.11. Coprolite directly dated
215	11,091–10,773 cal BP (9585 ± 20, UCIAM-S-76181)	1704-PC-5/12A-16-10	2.03 (I)	Very dark brown (7.5 YR 2.5/3), opaque	25.88 × 20.98 × 19.24	Cylindrical[d]	Fissure	Round stone, plant, hair	Hard	Sample 1704-PC-5/12A-16-10 with *Homo sapiens* haplogroup A mtDNA (Jenkins et al. 2012 Table S12)	Cave 5, Unit 12, quad A, LU 2. Elevation 1367.24. Coprolite directly dated
92	~ 10,850 cal BP	1896-PC-2/6A-48-2	5.4 (E)	Black (7.5 YR 2.5/1), opaque	65.96 × 26.92 × 23.52	Cylindrical	Fissure; vacuole; gallery hole	Plant, bone, tooth, insect	Hard		Cave 2, unit 6, quad A, LU 3. Elevation 1365.90. Estimated age based on stratigraphic position

[a] Previously published radiocarbon dates from Jenkins et al. 2013. Radiocarbon dates calibrated using IntCal 2013 (Reimer et al. 2013) in Oxcal 4.3 (Bronk Ramsey 2013)

[b] *(I)* = interior sample; *(E)* = exterior sample

[c] Combined age calculated using Oxcal 4.3 "R_combine" command

[d] Volume extrapolated from fragment(s)

The faunal analysis focused on both cranial and postcranial elements. Lab protocols and faunal identifications were conservative (Driver 2011; Gobalet 2001). Fauna identifications were completed under magnification (i.e., × 10, × 20, and × 40) with the aid of a stereomicroscope. Bird and mammal remains were identified using osteological comparatives housed at the Museum of Vertebrate Zoology, University of California, Berkeley. Fish remains were identified using an osteological collection housed in the Department of Anthropology, University of California, Berkeley and supplemented by specimens from the California Academy of Sciences Ichthyology Collection, San Francisco, California. This study follows the standard of Page et al. (2013) for scientific and common names of fishes. Osteological and NISP data were recorded for each skeletal specimen (Grayson 1984; Lyman 2008). Unidentified fragments < 0.25 mm are not included in the NISP counts. Taphonomic analysis of faunal remains follows the protocols outlined by Fisher Jr (1995) and Butler and Schroeder (1998).

Insect remains were examined under a dissecting microscope and identified to the highest resolution taxonomic classification possible using classification keys and other references (Bousquet et al. 2018; Doyen 1984; Fisher and Cover 2007; Hebard 1916; Young 1988), as well as online resources, including the Global Biodiversity Information Facility (https://www.gbif.org) and Harvard's Museum of Comparative Zoology (https://mcz.harvard.edu). Nomenclature follows Bousquet et al. (2018), Doyen (1984), and Fisher and Cover (2007). Voucher specimens are curated at the Oregon Museum of Natural and Cultural History archaeological research laboratory at the University of Oregon, Eugene.

Pollen analysis

The pollen subsample was acetolyzed (Erdtman 1960; Hesse and Waha 1989) to remove nonsporopollenin organic compounds, separated using sodium polytungstate calibrated to a density of 1.9 g/cm^3, stained with safranin, then stored in glycerol. A small amount of pollen sample was mounted with glycerol on a glass slide and analyzed using a light microscope at × 200 and × 400 magnification. Pollen analysis consisted of a minimum of 200 indigenous terrestrial and aquatic grain count, except for samples with poor pollen preservation (see below). A 200-grain count is standard protocol for coprolite studies and is adequate for samples with low taxonomic diversity (Faegri and Iversen 1989; Moore et al. 1991). Pollen recovered from the coprolites was compared to reference material at Newcastle University and the Garrett Herbarium at the Utah Museum of Natural History, published reference literature (Faegri and Iversen 1989; Kapp et al. 2000; Moore et al. 1991), and online pollen image databases (e.g., https://globalpollenproject.org; http://www.paldat.org). Pollen in the family Asteraceae was identified as either *Artemisia* type, low-spine, high-spine, or dandelion type following Martin (1963).

Aggregate pollen grains were counted as a single grain so that their frequency did not overwhelm the other taxa present in the sample (Sobolik 1988). The procedure was also necessary because it was not possible to get an accurate count of the number of grains in densely packed pollen aggregates. Pollen counts were converted to pollen frequency (percentage of the sum for each sample) to enable comparison between samples with variable total pollen counts (Faegri and Iversen 1989; Moore et al. 1991). Pollen concentration value per gram of coprolite sample was calculated using the formula below (following Benninghoff 1962 and Maher 1981). Approximate pollen concentrations for each taxon were calculated by multiplying total concentration value by relative frequency for each pollen taxon (Dean 1993). Pollen data is diagrammed using C2 stratigraphic software (Juggins 2007).

$$\frac{\text{Total indigenous pollen counted} \times \#L.clavatum \text{ added}}{\text{Weight in grams of sample} \times \#L.clavatum \text{ counted}}$$

Pollen can enter the human digestive system through multiple pathways—ambient pollen is in the air we breathe, the water we drink, and the food we eat (Bryant 1974b; Bryant and Holloway 1983; Martin and Sharrock 1964). Therefore, not all pollen recovered from fecal matter is linked to dietary choices. To address these potential biases, our analysis followed established criteria for linking pollen data with intentional dietary or medicinal consumption of plant material (Bryant 1974a, 1974b; Reinhard et al. 1991; Sobolik 1988).

Pollen aggregates for both anemophilous (wind-pollinated) and entomophilous (insect-pollinated) taxa often indicate intentional consumption of that taxa. Larger aggregates of a single pollen type typically represent consumption of pollen from the anther of a flower; smaller aggregates can indicate consumption of foliage and seeds of that taxon (Bryant 1974a).

Pollen produced by an entomophilous taxon and present in frequencies ≥ 4% (the typical upper frequency of entomophilous taxa in ambient pollen rain) and/or in concentration above the mean for that taxon across all samples provides evidence for intentional consumption of the flowers, buds, foliage, or seeds of that taxon (Dean 1993; Reinhard et al. 1991; Reinhard 1993; Sobolik 1988). Anemophilous taxa produce pollen in relatively high frequencies and are commonly incorporated into ambient pollen rain; therefore, linking frequencies of pollen from anemophilous taxa to intentional consumption is somewhat more problematic (Bryant and Holloway 1983; Martin and Sharrock 1964; Reinhard et al. 1991). However, ambient pollen should be represented in relatively equal amounts across a series of coprolites from the same site (Dean 1993; Reinhard et al. 1991). This study

compares the relative frequency and concentration of anemophilous taxa to the mean of that taxa across the entire series of coprolites as well as naturally derived paleoenvironmental samples from the study area to identify intentional consumption. High relative frequencies (> 40%) and concentrations (< 100,000 grains per gram of coprolite) of pollen from anemophilous taxa are considered to represent intentional consumption because frequencies and concentrations higher than this are not typically observed in naturally derived samples (Bryant 1974a; Reinhard et al. 1991).

Phytolith analysis

The phytolith subsample liquid was placed in a crucible and dried at 150 °C, then placed in a muffle furnace for 2 h at 500 °C to remove organic matter. Phytolith material was separated using sodium polytungstate calibrated to a density of 2.3 g/cm^3, then dried. A known weight of the resulting material was permanently mounted in Entellan mounting agent on a 22 × 22-mm slide. Phytoliths were analyzed with a light microscope at × 200 and × 400 magnification. Density of phytoliths per gram of coprolite was calculated by studying a known number of fields at × 400 magnification. At this magnification, there are 48 fields of view in one 22-mm column of the slide, which equals 2304 total fields of view on the slide. Density per gram was calculated employing the formula below and is used to compare relative inputs of plant material into the diet.

$$\text{Phytoliths per slide} = \left(\frac{\text{phytolith count}}{\text{fields counted}}\right) \times \text{total fields on slide}$$

$$\left(\frac{\text{phytoliths per slide}}{\text{phytoliths mounted (mg)}} \times \frac{\text{mass phytoliths extracted (mg)}}{\text{coprolite weight (mg)}}\right) \times 1000$$

Phytoliths were grouped into morphotypes based on three-dimensional shape. Phytolith counts consisted of between 200 and 300 single-cell and between 50 and 100 multicell phytoliths. If 300 single cells were counted before 50 multicell phytoliths were observed, then counting for that sample stopped. Previous studies have shown that counting 265 phytoliths with consistent morphology gives a 12% error margin (Albert and Weiner 2001). Phytolith counts were converted to relative frequency by dividing the count of morphological types by the total phytolith count for that sample enabling comparison between coprolites. Single-cell and conjoined phytolith counts are presented separately.

Monocotyledon plants (monocots) are dominated by members of the Orchidaceae (orchid) and Poaceae (grass) families. Most monocots produce abundant phytoliths, and particular species of grasses typically produce high frequencies of specific morphotypes (Blinnikov 2005; Twiss et al. 1969). Short-cell phytoliths are formed in specialized grass epidermis cells and lie across the veins of the leaf and leaf-derived tissues (e.g., glumes, husks) and sometimes in cells lying between the veins (Pearsall 2015, p. 256). Short cells are abundantly produced by grasses and may be very common in archaeological samples. Long-cell phytoliths are formed in nonspecialized grass epidermal cells. Length, wall thickness, and surface ornamentation of long cells are diverse, and they often have limited usefulness for distinguishing among grass species (Pearsall 2015, p. 256; Twiss et al. 1969). Trichome phytoliths and silicified hairs and bases typically form in epidermal appendages on grass blades (Blinnikov 2005). Dendritic long cells and scutiform/papillae phytoliths are formed in grass seed epidermal cells; these types are produced during the months tied to plant flowering and fruiting times and are therefore useful for assessing season of consumption (Harvey and Fuller 2005, p. 743).

Dicotyledon (dicots) plants are dominated by herbaceous forbs. Dicots generally produce lower frequencies of phytoliths than monocots (Piperno 1988). Studies of Great Basin taxa indicate this holds true for dicots from the study region (Morris et al. 2009). Epidermal polygonal phytoliths are typical of dicots but are also largely nondiagnostic from one taxon to the next (Pearsall 2015). Dicot samples collected in the Great Basin commonly produced hairs, anticlinal and polyhedral epidermal sheets, and tracheids (Morris et al. 2009).

Relative counts of the morphotypes described above are used to distinguish the consumption of monocot (e.g., grasses) and dicot (e.g., forbs) plant material and, when possible, to identify consumed plant parts within these broader plant groups. The morphotypes in this study follow those established for plant taxa common to the Pinyon-juniper woodlands and sagebrush grassland steppe of the Great Basin (Morris et al. 2009) and interior Pacific Northwest (Blinnikov 2005).

Results

Radiocarbon dating

This study presents new radiocarbon dates on three previously undated coprolites: two yielding calibrated radiocarbon ages in the YD period and one in the EH (Table 2). When combined with previously published dates and estimated ages based on stratigraphic provenience, the nine coprolites presented here broadly cluster into YD-aged occupations (12,800–11,700 cal BP) represented by six samples and EH-aged occupations (11,200–10,850 cal BP) represented by three samples (Fig. 5).

Table 2 New radiocarbon dates on Paisley Caves coprolites. Radiocarbon dates calibrated using IntCal 2013 (Reimer et al. 2013) in Oxcal 4.3 (Bronk Ramsey 2013)

Coprolite sample	Material	$\delta^{13}C$ (‰)	^{14}C BP	Cal BP (2σ)	Laboratory number
98	Bulk sample: uncharred, unidentified plant fiber	− 22.43	10,407 ± 37	12,515–12,087	OxA-38445
55	Bulk sample: charcoal and uncharred, unidentified plant fiber	− 25.91	10,262 ± 57	12,376–11,767	OxA-38674
242	Bulk sample: charcoal and uncharred, unidentified plant fiber	− 23.43	9663 ± 29	11,196–10,823	OxA-38415

Plant and faunal macrofossil analysis

Table 3 provides a summary of results for all coprolites analyzed for this study. A variety of plant, animal, and stone material was recovered from each of the nine coprolites (Table 4). Plant fiber was present in all samples, consisting of anywhere from 0.3 to 69.15% of the total macrofossil weight. Sand to pebble-sized angular to round stone was present in all samples, including interior samples not in contact with the surrounding matrix. The diversity of plant remains across the nine coprolites is notable; there are very few identified taxa that repeat from one coprolite to another. Seed was present in six coprolites, although in low frequencies (Fig. 6). Coprolite 56 contained *Rosa* cf. *woodsii* (Wood's rose) seed and possible fruit skins likely representing consumption of rose hips (Fig. 7a). Coprolites 57 and 242 contained *Typha* sp. (cattail) seed (Fig. 7e), coprolite 242 contained *Carex* sp. (sedge) seed (Fig. 7g), coprolite 98 contained cf. Amaranthaceae (amaranth family) seed (Fig. 7d), coprolite 215 contained cf. *Amaranthus* sp. (amaranth) (Fig. 7f) and cf. *Descurainia pinnata* (tansy mustard) seed (Fig. 7b), coprolite 92 contained cf. Poaceae (grass family) caryopses that appear to have been significantly impacted by food processing and/or digestion (Fig. 7c), and coprolites 92 and 98 contained unidentified seed types. None of the seeds appear to be carbonized.

Faunal material was recovered in each of the nine coprolites (Table 5, Fig. 8). Most of the faunal material was highly fragmented with evidence of digestive processes, especially acid-etching and rounding, and could only be identified to broad categories. Identified taxa include *Lepus* sp. (hare/jackrabbit) (Fig. 9a), Rodentia (Fig. 9b–d), Catostomidae/Cyprinidae (fish), and Aves (bird). Rodentia bones are linked with a significant amount of animal hair in coprolite 56.

Eight of the Paisley coprolites contained insect remains (Table 6, Fig. 10), many of which could not be securely identified because they were too damaged from processing and/or digestion. The majority of insect remains were recovered from coprolite 92 and include remains from *Polyphylla* cf. *decemlineata* (ten-lined June beetle) (Fig. 11a), *Stenopelmatus* cf. *fuscus* (Jerusalem cricket), and the remains of individuals in the family Tenebrionidae (darkling beetles), including *Eleodes obscura sulcipennis* (Fig. 11b) and *Eusattus muricatus* (Fig. 11c). Coprolite 92 contained many unidentified

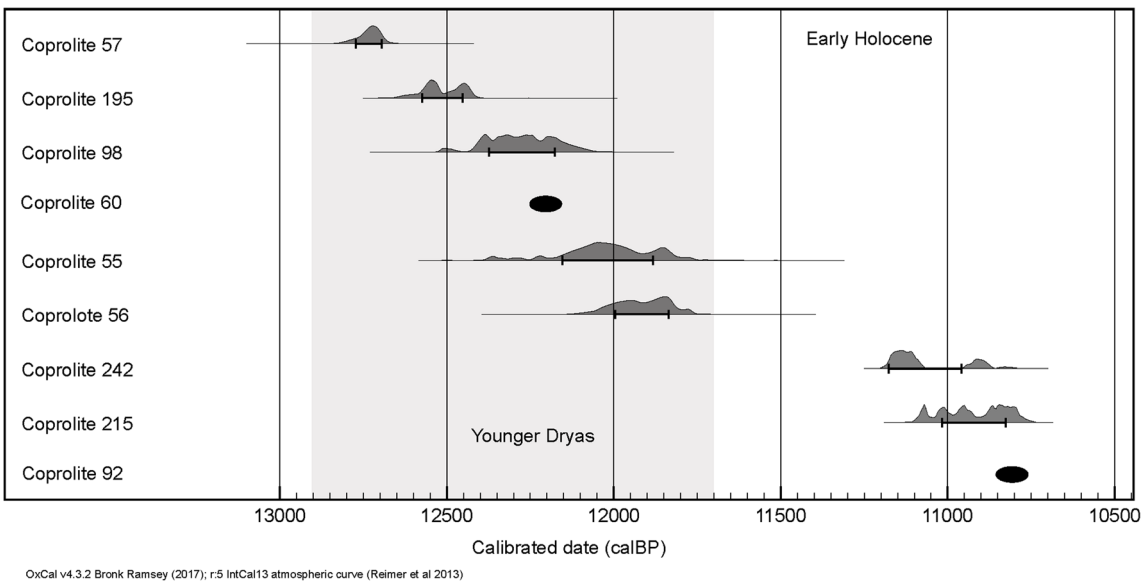

Fig. 5 Age of the nine coprolites presented in this study: gray distribution curves represent calibrated radiocarbon age; black ovals represent estimated age based on stratigraphic position. Coprolite 195 combined age calculated using Oxcal 4.3 "R_combine" command (Bronk Ramsey 2013)

Table 3 Results of multiproxy analysis showing dietary items represented in each coprolite, ecological foraging zone, and inferred season of occupation. Samples are listed from oldest to youngest

	Younger Dryas						Early Holocene		
	57	195	98	60	55	56	242	215	92
High confidence of consumption	Dicot plant material (H); hare/jackrabbit (M); cattail seed (M)	Monocot and dicot plant material (P); unknown mammal or bird (M); legume flowers (P)	Monocot plant material (H); small/medium mammal likely rabbit or hare (M); bird (M); dicot plant material/-amaranth seed (M, H); unidentified seed (M)	Monocot and dicot plant material (H); unknown vertebrate animal (M); fish (M)	Monocot and dicot plant material (H); unknown mammal or bird (M); monocot seed husk/grass family plant material (H, P)	Monocot and dicot plant material (H); rodent (M); rose fruit (M)	Monocot and dicot plant material H); bird (M); cattail seed (M, P); sedge seed (M, P)	Monocot and dicot plant material (H); unknown mammal (M); amaranth seed (M, P); tansy mustard seed (M); buckthorn plant material (P)	Monocot and dicot plant material (H); rodent (M); Jerusalem cricket (M); ten-lined June beetle (M); darkling beetles (M); evening primrose plant material (P); grass seed (M); unidentified seed (M)
Moderate confidence of consumption		Pondweed plant material (P)	Sagebrush plant material (P); cattail plant material (P)		Willow plant material (P)	Bird (M); beetle (M)	Willow plant material (P); plantain plant material (P)	Willow plant material (P); wild buckwheat plant material (P); aster family plant material (P); beetle (M)	Sagebrush plant material (P); willow plant material (P)
Ecological foraging zone[a]	Wetlands (cattail); sagebrush steppe (hare)	Aquatic (pondweed)	Wetlands (cattail), sagebrush steppe (sagebrush, amaranth)	Lacustrine/riparian (fish)	Wetland/riparian (willow)	Upland riparian/-sagebrush steppe (rose)	Wetland (cattail, sedge), wetland/-riparian (willow)	n/a	Sagebrush steppe/grassland (grass, sagebrush); wetland (willow)
Inferred season of occupation[a]	Summer/fall (cattail seeds mature)	Spring/summer (flowers mature)	Late summer/fall (amaranth seeds mature)	n/a	Summer/fall (seed husk growth)	Summer/fall/winter (rose hips mature)	Summer/fall (cattail, sedge seeds mature)	Fall (pigweed), summer (tansy mustard)	Summer/fall (grass seed matures). Late spring to early fall (Jerusalem cricket life cycle)

P = pollen data, *H* = phytolith data, *M* = macrofossil data

[a] Information on plant habitat and life cycles from the USDA PLANTS Database

Table 4 Weight (mg) of macrofossil categories in the Paisley coprolite < 250-μm fraction. MNI seed counts presented in parentheses. Samples are listed from oldest to youngest

	Inorganic				Faunal				Plant bulk			
	Angular pebble spall	Obsidian	Stone	Charcoal	Bone	Insect	Hair	Feather	Plant fiber	Coarse plant fiber (stems/bark)	Misc. plant	Possible fruit skin
57			16.3	T	550	T			10.7	1.3	–	
195			16.8		T	T			37.6		T	
98			1138.3	1.4	1809.3	T		92.9	236.3	24.6	0.4	
60			0.9	1.2	61.2		T		2	0.9		
55			3.6	0.7	10	2.2			2.6	0.5	T	
56			107.7	0.7	129.6	0.8	44.1	1.7	44.9	20.5	3.6	2.1
242	431.7		224.3	3.2	50.4		0.7	50.7	15.1		1	
215		L	406.9		1.1	0.7			50	45.7	2.5	
92			879.1		7	532.7	T		5.4	16.8	1	

	Seeds								
	Rosaceae *Rosa* cf. *woodsia* seed	Typhaceae *Typha latifolia* seed	cf. Poaceae caryopsis	Unidentified seed	Cf. Amaranthaceae	Amaranthaceae cf. *Amaranthus* sp. seed	Brassicaceae *Descurainia* cf. *pinnata* seed	Cyperaceae *Carex* sp. seed	Miscellaneous	Total
57		T (1)								578.3
195										54.4
98				T (1)	T (1)					3303.2
60										66.2
55										19.6
56	20.5 (7)								24.4[a]	400.6
242		T (7)						0.3 (1)		777.4
215						T (2)	T (1)			506.9
92			0.1 (9)	0.7 (5)					467.2[b]	467.2

T = trace amounts < 0.09 mg; *L* = sample lost before it could be weighed

[a] Fine plant fiber and animal hair that could not be separated

[b] Primarily very small and highly fragmented insect remains, but also contains very fine hair, plant fiber, and sand that were not possible to be separated

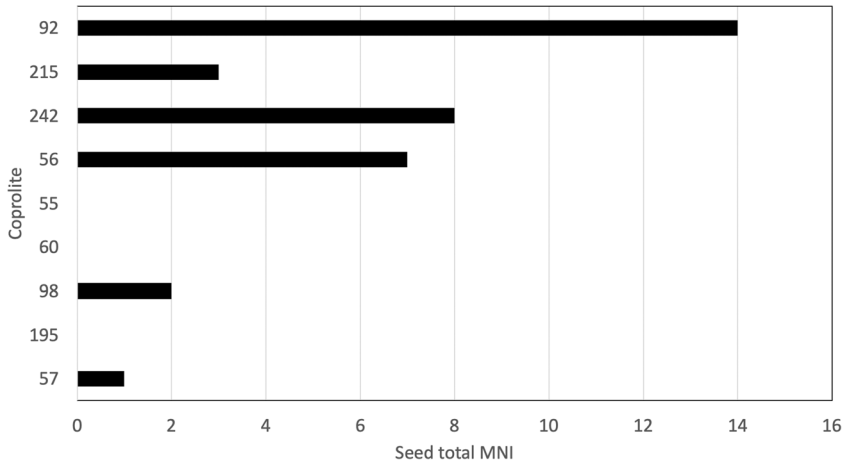

Fig. 6 Bar chart showing total seed MNI in each coprolite

remains of tenebrionids that are likely additional fragments of *Eusattus* or *Eleodes*. Coprolites 56 and 215 contained remains of individuals from the order Coleoptera.

Coprolites 56 and 195 contained remains of very small ants, likely from the genus *Camponotus* (carpenter ants). Coprolites 55 and 57 contained larval fly (maggot) puparium fragments. 470 insect elements or fragments—primarily from coprolite 92—were classified as indeterminate order; most of these elements are likely linked to the taxa described above.

Pollen

Coprolites 55, 56, 57, 60, 92, and 195 were processed with both interior and exterior coprolite material, so the pollen counts for these coprolites may contain pollen from the surrounding soil matrix in addition to pollen from the digestive system of the individual. However, this should only introduce pollen types already present in the ambient pollen rain, and the introduced grains should not exceed ambient levels for these taxa. Coprolite pollen data are compared to previously published pollen frequencies in YD- and EH-aged sediment

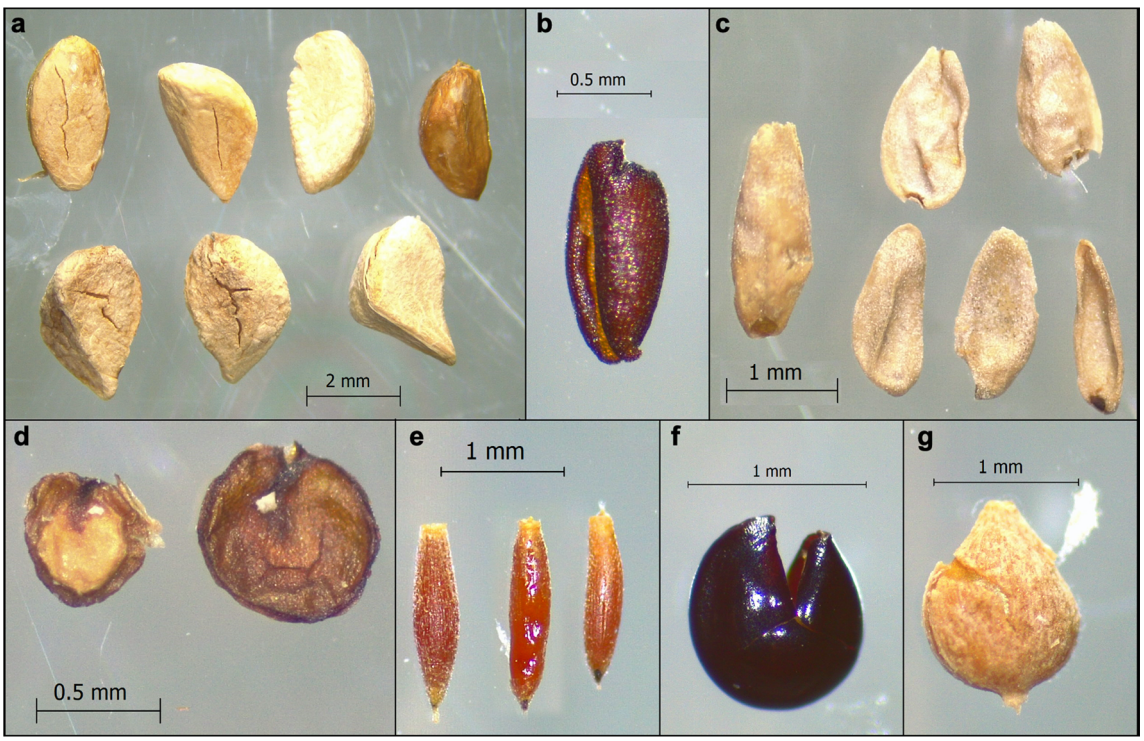

Fig. 7 Plant macrofossils identified from the Paisley Caves coprolites: **a** coprolite 56 *Rosa* cf. *woodsii* seeds, **b** coprolite 215 cf. *Descurainia pinnata* seed, **c** coprolite 92 cf. Poaceae caryopsis, **d** coprolite 98 cf. Amaranthaceae seeds, **e** coprolite 242 *Typha* sp. seeds, **f** coprolite 215 cf. *Amaranthus* sp. seed, **g** coprolite 242 *Carex* sp. seed. Complete macrofossil data is presented in the supplementary material (Online Resource 1)

Table 5 Summary table of faunal remains recovered from Paisley coprolites

Taxon	57 NISP	195 NISP	98 NISP	60 NISP	55 NISP	56 NISP	242 NISP	215 NISP	92 NISP	Total NISP
Vertebrata		2		87						89
Mammalia/Aves	36		244		3	230				513
Mammalia								43		43
Lepus (hare/jackrabbit)	1									1
Small/medium mammal			4							4
Very small/small mammal									62	62
Rodentia						15			4	19
Actinopterygii										
Catostomidae/cyprinidae (fish) very small				1						1
Aves							35			
Total	37	2	248	88	3	245	35	43	66	767

samples collected in the Paisley Caves as well as modern surface samples collected in a 50-km^2 region surrounding the Paisley Caves (Beck et al. 2018). These data establish a baseline expectation for ambient pollen rain frequencies.

All nine of the Paisley coprolites contained pollen (Fig. 12), but coprolites 57 and 60 did not contain autochthonous pollen in any meaningful amount and are not discussed further. Pollen count, frequency, concentration, and aggregate data are presented in the supplementary material (Online Resource 1). Total pollen concentration in the remaining seven samples was variable, ranging from 29,373 to 288,075 grains per gram of coprolite material, well above the 1000 grains per gram concentration suggested for reliable results in sediment samples (Bryant and Hall 1993). The following results highlight patterns in the pollen data that fit the criteria for intentional consumption established above.

Coprolite 195 contained 8% of a single type of entomophilous Fabaceae (legume) pollen (Fig. 13a), including eight aggregates estimated to contain more than 1130 grains (Fig. 13b). *Potamogeton* sp. (pondweed) pollen is anemophilous and present in relatively low frequency (3%), but this taxon is not represented in any coprolites in this study or in previously published coprolite and sediment samples from the Paisley Caves (Beck et al. 2018; Cummings et al. 2007; Taylor et al. 2019).

Coprolite 98 contained a single aggregate of approximately 30 anemophilous *Typha latifolia* (cattail) pollen grains (Fig. 13c) and contained 15% *Typha* pollen when the aggregate count is included, well above the mean for all coprolites and the frequency in sediment samples collected in and outside of Paisley Caves. Coprolite 98 also contained a single aggregate of *Artemisia* pollen containing approximately six grains, and the frequency of *Artemisia* pollen (43%) is more than double the mean of *Artemisia* across all coprolites. *Artemisia* can be entomophilous but is more commonly anemophilous. Coprolite 55 contained 13% anemophilous Poaceae pollen in a concentration of 4394 grains per gram—above the mean for the entire coprolite series. Poaceae pollen is not present in amounts exceeding 5% in sediment samples from the caves but comprises up to 30% of the pollen rain outside of the caves. *Salix* sp. (willow) pollen represents 4% of the total pollen in coprolite 55. *Salix* is typically

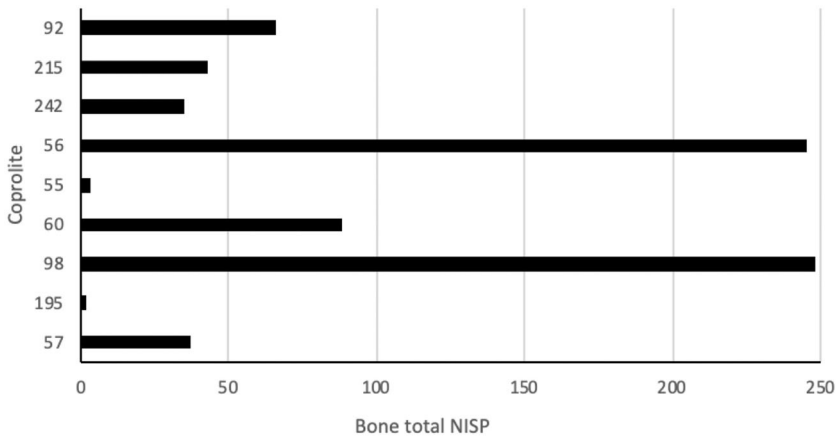

Fig. 8 Bar chart showing total bone NISP in each coprolite

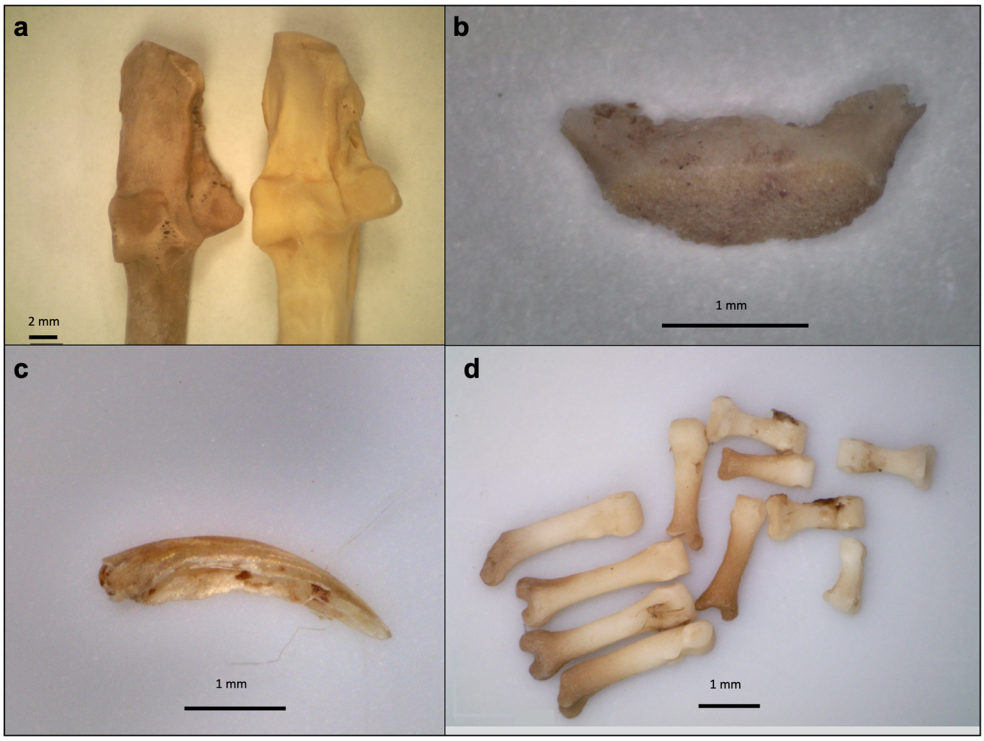

Fig. 9 Faunal material identified in the Paisley Caves coprolites: **a** Coprolite 57 *Lepus* sp. calcaneus (left is the coprolite specimen and right is the reference specimen—note acid modification on coprolite specimen). **b** Coprolite 92 Rodentia vertebra fragment. **c** Coprolite 56 Rodentia corpus unguis. **d** Coprolite 56 Rodentia phalanges

entomophilous pollinated (Reinhard et al. 1991), and *Salix* is present in amounts less than 1% in sediments collected in and outside of the caves. However, the mean frequency for *Salix* pollen across all coprolites is 4%, suggesting that this may represent ambient levels of this pollen type.

Coprolite 242 contained high frequency and concentration of anemophilous Cyperaceae (sedge) and *Typha latifolia* pollen compared to the mean for all coprolites and sediment samples collected in and outside of the caves. *Salix* pollen is present in a frequency well above the mean (14%) including an aggregate of ~ 10 grains. Coprolite 242 also contained 9% *Plantago* sp. (plantain) pollen (Fig. 13d); this genus is typically anemophilous (Faegri and Iversen 1989; Sharma et al. 1993), but it is not present in other coprolites in this study or in sediment samples.

Coprolite 215 contained high frequency and concentration of anemophilous Amaranthaceae pollen compared to the mean for all coprolites, including a single aggregate of four grains, and a high concentration of anemophilous low-spine Asteraceae pollen grains, including a large aggregate of ~ 32 grains (Fig. 13e). Coprolite 215 also contained a high frequency (13%) of single type of entomophilous Rhamnaceae (buckthorn family) pollen (Fig. 13f), entomophilous *Eriogonum* (buckwheat) pollen in a frequency and concentration above the mean for all coprolites and sediment samples, and *Salix* in high concentration relative to the mean for all coprolites. Coprolite 92 contained a high frequency of entomophilous Onagraceae cf. *Chamerion* type pollen (Fig. 13g) and *Salix* pollen, as well as a high frequency of *Artemisia* pollen compared to sediment samples, including an aggregate comprised of six grains.

Phytoliths

Phytoliths in the Paisley Caves coprolites are well-silicified, indicating the region was favorable for phytolith development and preservation. Most of the coprolites contained phytolith morphotypes representing both monocot and dicot plant types, in particular epidermis (leaf) material from these two plant types (Fig. 14, Online Resource 1). Phytolith density was variable between samples, ranging from an estimated 119 to 476,370 phytoliths per gram of coprolite (Fig. 15). The phytolith samples from coprolites 55, 56, 60, 92, and 215 primarily consist of morphotypes representing monocot epidermal material (Fig. 16), including conjoined phytoliths representing monocot epidermal sheets (Fig. 17a, b). These five samples also contained phytolith morphotypes representing dicot epidermal material but in lesser amounts (Fig. 17c). Coprolite 55 contained a high frequency of monocot morphotypes and a small number of single and conjoined dendritic phytoliths representing grass seed husks (Fig. 17d). The phytolith samples from coprolites 98 and 195 are more evenly split between phytoliths representing monocot and dicot epidermal material (Fig. 17e–g). The phytolith sample from coprolites 57 and 242 primarily consists of morphotypes representing dicot epidermal material (Fig. 17g).

Table 6 Summary table of insect remains recovered from Paisley coprolites. Samples are listed from oldest to youngest

Order	Orthoptera (grasshoppers, crickets)		Coleoptera (beetles)										Hymenoptera (wasps, bees, ants)		Diptera (flies)		Indet order		Total	
Family	Stenopelmatidae		Scarabaeidae		Tenebrionidae						Indet. family		Formicidae		Indet family					
Genus/species	*Stenopelmatus* cf. *fuscus*		*Polyphylla* cf. *decemlineata*		*Eleodes* (*Eleodes*) *obscura sulcipennis*		*Eusattus muricata*		Indet. genus/species				cf. *Camponotus* sp.							
Common name	Jerusalem cricket		Ten-lined June beetle		Desert stink beetle		n/a						Carpenter ant							
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
57															4	3			4	3
195													4	1					4	1
98																	2	1	2	1
60																			0	0
55															40	5			40	5
56											1	1	6	1					7	2
242																			0	0
215											3	1							3	1
92	16	3	439	6	39	3	13	1	53	0							468	2	1028	15

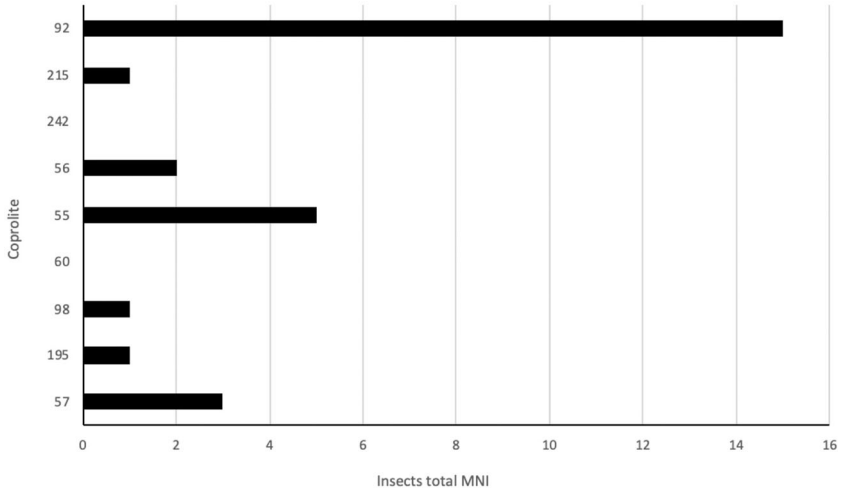

Fig. 10 Bar chart showing insect MNI in each coprolite

Discussion

The multiproxy macro and microscopic analyses presented in this study provide new data on YD/EH diet, season of occupation, and land-use patterns during the WST occupation at Paisley Caves in the northern Great Basin. This study presents a relatively small data set considering the 2000 years of occupation represented by the coprolites but provides crucial data for this poorly represented time period. As data improves both from the Paisley Caves and other sites in the region, we will have the opportunity to further explore ongoing debates about WST diet and land use.

Human origin of coprolites

During rehydration, coprolites 92, 215, 242, 56, 55, 60, and 98 turned the sodium phosphate solution opaque to semi-opaque with colors ranging from black to dark brown—consistent with human origin (Bryant 1974b). These seven coprolites contained a variety of plant macrofossils and animal bone suggesting an omnivorous diet. Coprolites 56, 92, and 215 had insect remains further representing an omnivorous diet, and all but 92 and 215 contained charcoal suggesting cultural food preparation. These characteristics led to the interpretation that humans deposited these seven coprolites. Sample 215 was previously found to contain *Homo sapiens* haplogroup A mtDNA (Jenkins et al. 2012), and recent fecal biomarker analysis has confirmed that this coprolite was deposited by a human (Shillito et al. 2020b).

During the rehydration process, coprolite 195 turned the sodium phosphate solution translucent and dark yellowish-brown—consistent with carnivore or herbivore origin (Bryant 1974b). The macrofossils recovered from coprolite 195 consist primarily of unidentified plant fiber; no seeds or charcoal were present in the analyzed sample. Pollen data indicate consumption of legume family flowers, and the phytolith data suggest the consumption of a high amount of monocot and dicot vegetation relative to the other coprolites. The coprolite also contained two small fragments of bone suggesting an omnivorous diet. Coprolite 195 was previously identified as human based on the presence of *Homo sapiens* haplogroup B2 mtDNA, though it also contained *Canis lupus/familiaris* mtDNA (Gilbert et al. 2008). Fecal biomarker analysis of coprolite 195 indicates the presence of fecal material from both human and carnivore sources suggesting coprophagy (Shillito et al. 2020b). The macrofossil and microfossil evidence suggest an omnivorous human-like diet, and the coprolite has very little hair or bone as would be expected in a carnivore coprolite. We do not expect that humans were consuming carnivore feces. It is possible that coprolite 195 represents feces deposited by a carnivore that consumed a meal consisting of human feces, in which case it still represents a record of human diet.

During the rehydration process, coprolite 57 also turned the sodium phosphate solution translucent and dark yellowish brown consistent with carnivore or herbivore origin. However, this coprolite contained a variety of plant material including plant fiber, cattail seed, phytoliths from dicot leaf material, and charcoal, as well as animal bone indicating the consumption of rabbit/hare. These constituents suggest an omnivorous diet and human origin for this coprolite and support research indicating that rehydrated color is not always an accurate indicator of herbivore, carnivore, or human origins (Reinhard and Bryant Jr 1992). Based on the characteristics described here we, are interpreting the nine coprolites in this study to be of human origin; this will be confirmed through forthcoming fecal biomarker analysis.

YD and EH diets

All nine coprolites in this study contained a mix of plant and faunal remains, though in varying proportions. Not all items that enter the human digestive system are necessarily linked to dietary consumption, some remains likely represent unintentional or incidental consumption. Sample 242 contained an angular pebble spall with the

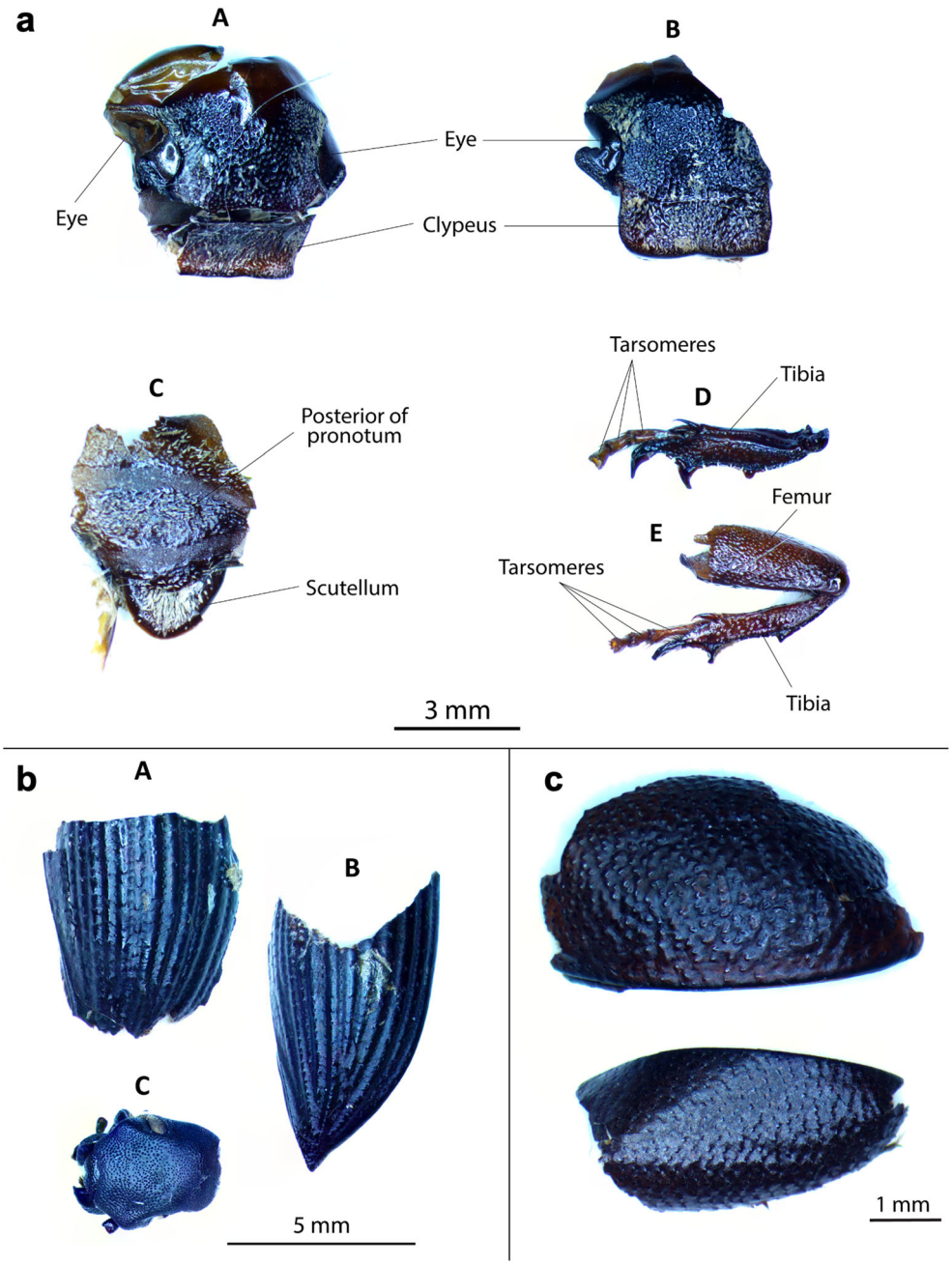

Fig. 11 Insect taxa identified in the Paisley Caves coprolites: **a** remains of the ten-lined June beetle (*Polyphylla* cf. *decemlineata*) recovered from coprolite 92: (A and B) frontal view of two head fragments; (C) dorsal view of the apex of a pronotum fragment and attached scutellum; (D) tibia and three attached tarsomeres of a foreleg; and (E) articulated femur, tibia, and three tarsomeres of a mid-leg; **b** remains of *Eleodes obscura sulcipennis* recovered from coprolite 92: (A) unsided elytrum fragment; (B) posterior fragment of the right elytron; and (C) dorsal view of the head; **c** two unsided elytra fragments of *Eusattus muricatus* recovered from coprolite 92

appearance of thermally fractured rock, possibly linked to stone cooking techniques. Sample 215 contained a very small obsidian retouch chip likely from hunting/processing tools. Small quantities of feathers and hair may also represent incidental consumption. Jenkins et al. (2016) suggest that food preparation at the Paisley Caves occurred on mats placed on the floor of the caves, which is a possible explanation for the introduction of material such as sediment, stone, hair, and feathers into foods prepared and consumed in the caves.

Bone inclusions in coprolites are likely to represent intentional consumption of meat. The faunal record provides evidence for consumption of small/medium and very small mammals, as well as birds and fish. The latter are represented by a single incidence of Catostomidae/Cyprinidae vertebra, indicating some use of lacustrine or riparian resources, likely procured from Summer Lake, the Chewaucan River, or Upper Chewaucan Marsh. Bone and feathers in coprolite 242 and feathers in coprolite 98 indicate bird was consumed, but more detailed taxonomic information is not available due to the absence of diagnostic skeletal elements. The small number of feathers in coprolite 56 provides moderate confidence of bird consumption but may represent accidental consumption. Notably, none of the bones in this study appear to have been

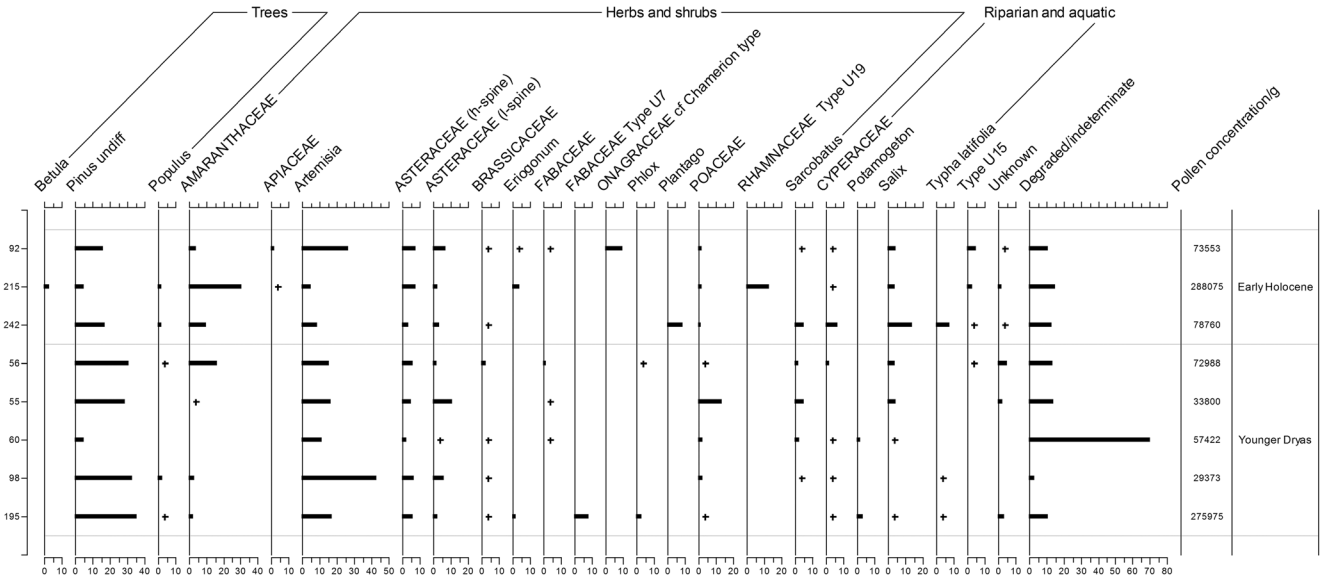

Fig. 12 Summary diagram of pollen relative frequencies for each taxa identified in this study. "+" indicates taxa present in frequency of 1% or less. Complete pollen data is presented in the supplementary material (Online Resource 1)

altered by cooking. The small, fragmented nature of the faunal assemblage precludes any in-depth interpretation of this observation, but future research may be able to infer food preparation methods from larger data sets like this.

Two coprolites provide evidence for consumption of hare/jackrabbit and small/medium mammal likely to be rabbit or hare. This supports previous studies suggesting that leporids were a common YD/EH dietary item at the Paisley Caves (Hockett et al. 2017; Taylor et al. 2019). Faunal

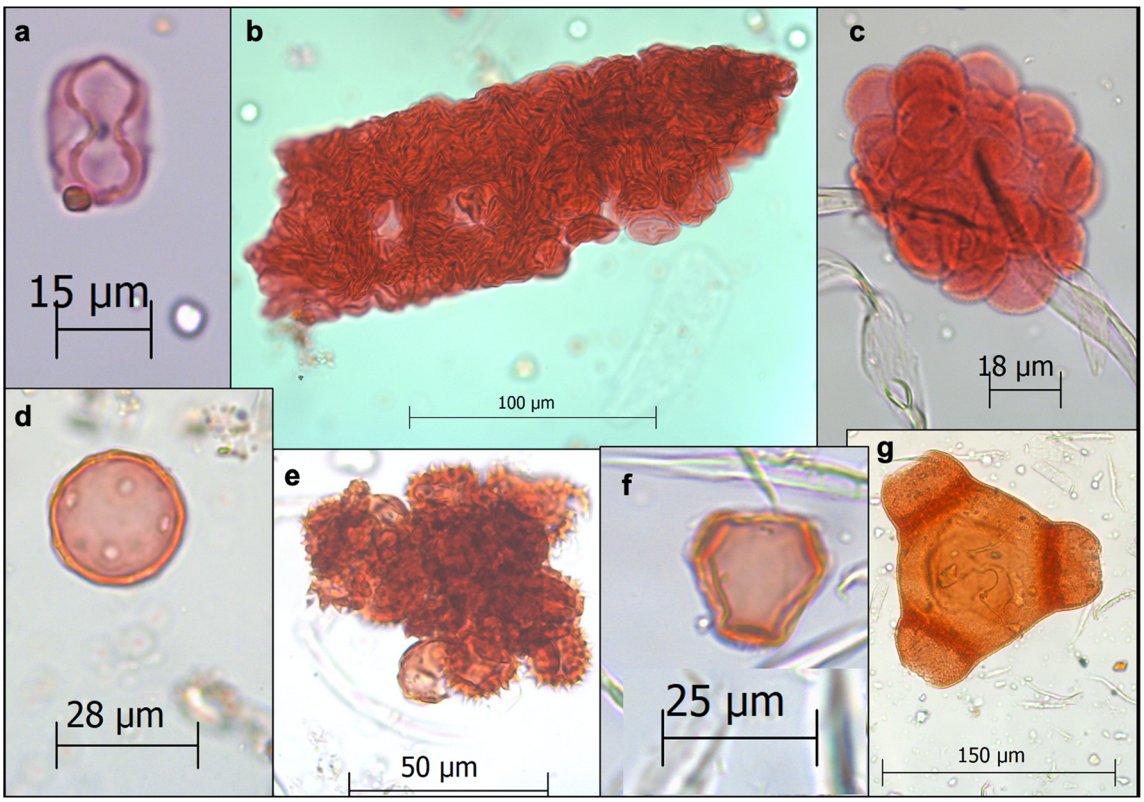

Fig. 13 Pollen grains identified in the Paisley Caves coprolites: **a** coprolite 195 Fabaceae type U7, **b** coprolite 195 Fabaceae type U7 anther aggregate, **c** coprolite 98 *Typha latifolia* aggregate, **d** coprolite 242 *Plantago* sp., **e** coprolite 215 low-spine Asteraceae aggregate, **f** coprolite 215 Rhamnaceae type U19, **g** coprolite 92 Onagraceae cf. *Chamerion* type

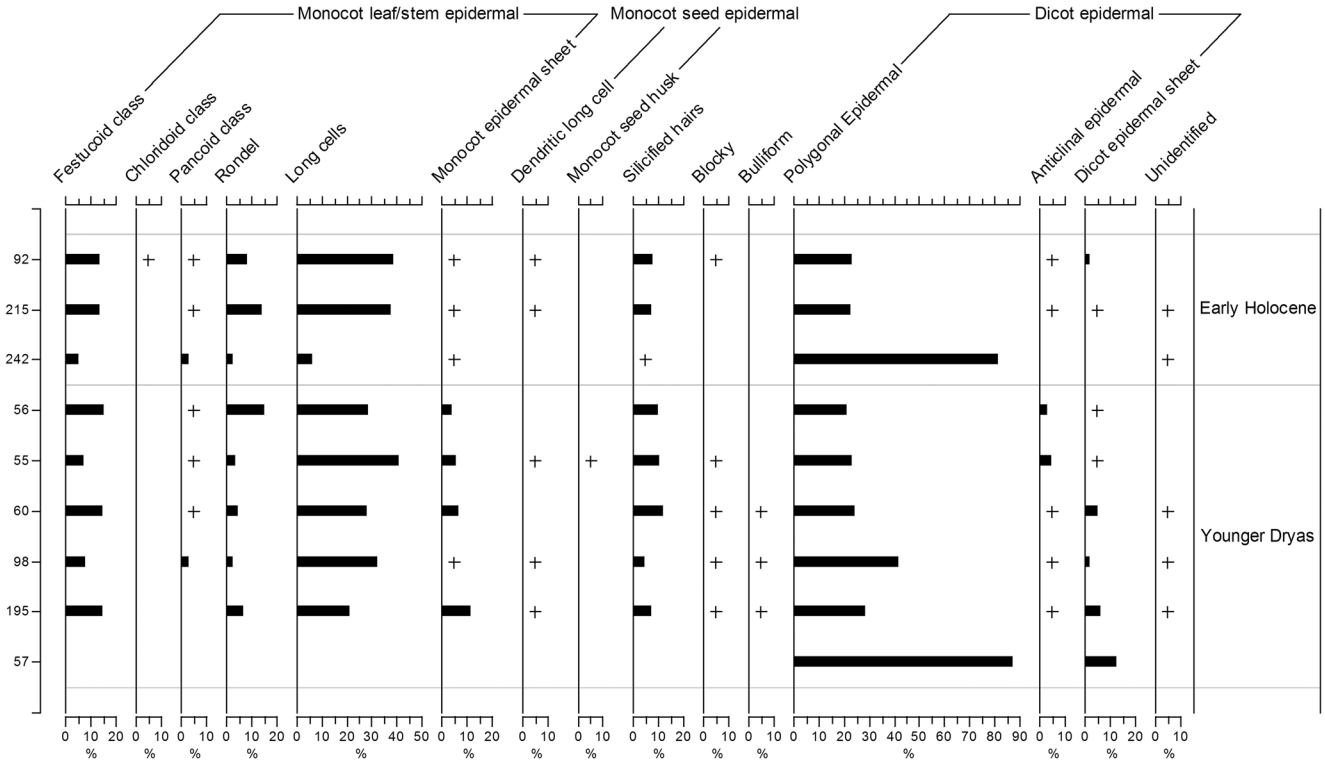

Fig. 14 Summary diagram of phytolith frequencies for each morphotype categories identified in this study. Frequencies are calculated as percent of total phytolith counts (single + conjoined with each conjoined sheet counted as one). "+" indicates morphotype category present in frequency of 2% or less. Complete phytolith data is presented in the supplementary material (Online Resource 1)

remains from rodent and rodent-sized mammal are present in two coprolites. The presence of rodent vertebra, phalanges, and corpus unguis along with animal hair in coprolite 56 suggests consumption of whole rodents including appendages, skin, and fur. Rodent consumption has been previously documented in ethnographic accounts and Holocene archaeological contexts in the Great Basin (Fowler 1986; Fry 1976; Reinhard et al. 2007), including in early and late Holocene occupations at the Paisley Caves (Taylor et al. 2019). Our analysis is the first study to present direct evidence for rodent consumption in the YD occupation of the Paisley Caves and, to our knowledge, for the broader northern Great Basin.

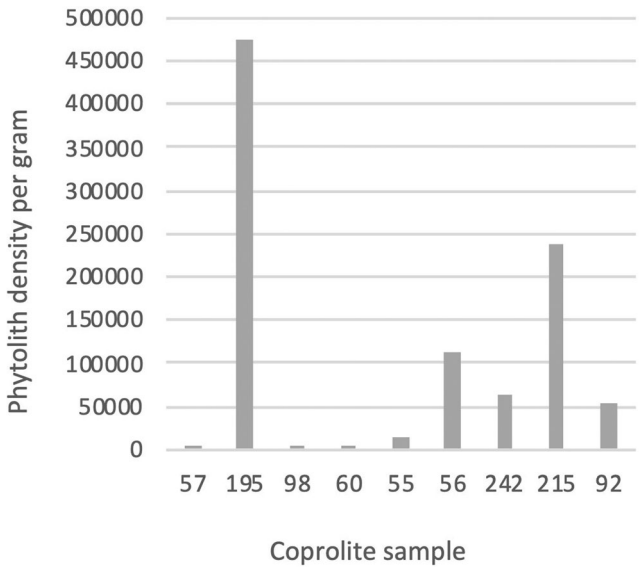

Fig. 15 Bar chart showing estimated phytolith density per gram of coprolite material

The faunal NISP is highly variable ranging from 2 to 248; two coprolites with high NISP have faunal material from fish (60) and rodent (56), suggesting a link between NISP and consumption of small animals that should be explored with larger data sets. Sample 98 has the largest NISP and largest initial sample weight, so faunal NISP may in some cases simply be correlated to sample size. NISP also likely reflects the variable impact of food processing and digestion (O'Meara 2014). Most of the faunal material can only be identified with coarse taxonomic resolution potentially masking the diversity of animal species consumed during the YD/EH.

Insect remains are linked to intentional consumption based on previous archaeological and ethnographic research, the behavior of the taxa identified, and the MNI and condition of the remains represented in the coprolite. All high-confidence evidence for consumption of insects comes from EH coprolite 92. The observation of the ten-lined June beetle remains is unique; this species has not been identified in previous studies of insect remains

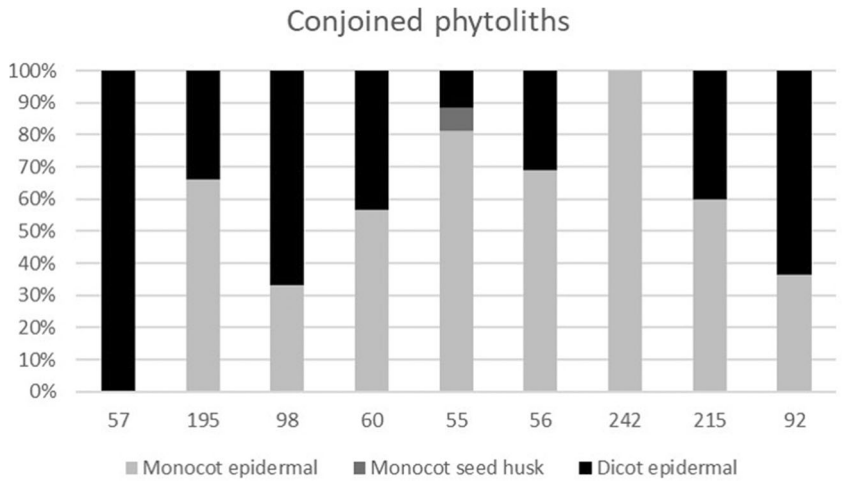

Fig. 16 Bar chart showing percent contribution of conjoined phytolith morphotype categories

recovered from archaeological contexts at the Paisley Caves (Adams, unpublished data; Hockett et al. 2017). This beetle is widespread in western North America; the larval period can last from 2 to 4 years, but the adult stage is relatively short, usually from late June to early October (Beers et al. 1993). Consumption of roasted adult June beetles is documented ethnographically by groups such as the Bear River Shoshone and Northern Paiute groups in California (Nomland 1938; Sutton 1988). Ten-lined June beetles are a relatively large species; they are attracted to lights and these particular specimens may have been caught and eaten after flying toward a campfire (Young 1988).

Jerusalem cricket remains have previously been recovered in YD-aged deposits at the Paisley Caves and were likely a common component of YD and EH diet (Hockett et al. 2017). Jerusalem cricket nymphs usually appear in the fall and can take up to 2 years to reach full maturity (Ebeling 1986). Jerusalem cricket remains are plentiful throughout the cave 2 insect assemblage (Adams, unpublished data). The use of Jerusalem crickets as a food source at the Paisley is unique as there is little or no evidence in the literature that supports

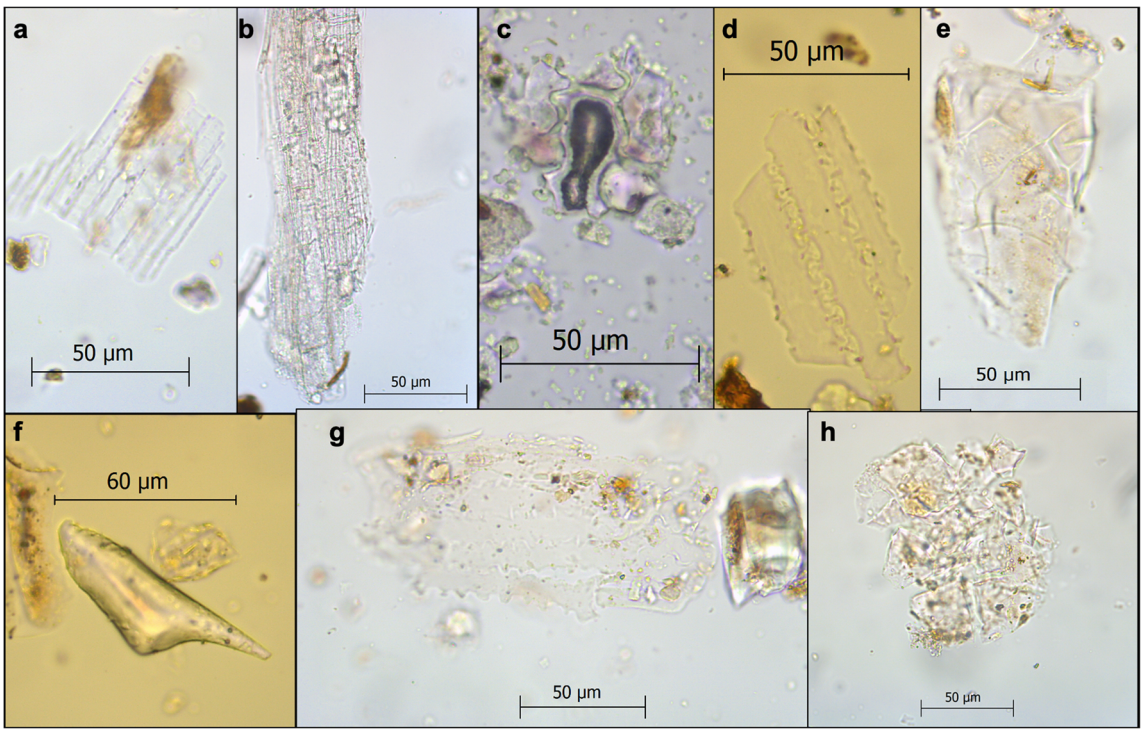

Fig. 17 Phytolith morphological types identified in the Paisley Caves coprolites: **a** coprolite 55 monocot epidermal sheet, **b** coprolite 60 monocot epidermal sheet, **c** coprolite 215 dicot epidermal sheet, **d** coprolite 55 monocot seed husk sheet, **e** coprolite 98 dicot epidermal sheet, **f** coprolite 98 trichome, **g** coprolite 195 monocot epidermal sheet, **h** coprolite 57 dicot epidermal sheet

them being a food source for Native peoples anywhere else in the Great Basin. While Mormon crickets (*Anabrus simplex*) tend to be a common insect food item when discussing Great Basin insect consumption (Ebeling 1986; Sutton 1988, 1995), preliminary analysis of the Paisley Cave 2 insect fauna indicate the abundance of Jerusalem crickets dominates that of Mormon crickets by a factor of 12 (Adams, unpublished data).

Darkling beetle remains are present in large quantities in the Paisley Caves deposits, and many members of this family are specifically adapted to living in arid environments such as those in the Great Basin. Both *Eusattus muricatus* and *Eleodes obscura sulcipennis* are generalist herbivores and scavengers (Aalbu et al. 2002; Doyen 1984) and may be attracted to fresh feces for its water content. The condition of both species in this assemblage, however, suggests they were most likely chewed and swallowed. The presence of *Eusattus muricatus* is not unexpected, as the remains of dozens of *E. muricatus* specimens have been recovered from the cave 2 deposits and it would appear they were quite plentiful (Adams, unpublished data). The presence of *Eleodes obscura sulcipennis* is, on the other hand, unusual. The common name for all members of the genus *Eleodes* is the "desert stink beetle," so named because these beetles possess a stink gland that is used to ward off potential predators and they have a reputation for being distasteful. However, the desert stink beetle does have medicinal uses among some arid-dwelling people, most notably the Navajo (Wyman and Bailey 1964), so human consumption may be linked to medicinal use.

Coprolites 56 and 215 contained remains of individuals from the order Coleoptera and may represent additional examples of intentional insect consumption similar to those documented in coprolite 92; however, these remains occur in low frequency and can only be attributed to intentional consumption with moderate confidence. Without higher-resolution identification, postdepositional intrusion into the coprolite by coprophagous beetles cannot be ruled out. Ant remains in coprolites 56 and 195 may represent intentional consumption, but the low frequency suggests accidental consumption or postdepositional intrusion into the coprolite. Coprolites 55 and 57 contained larval fly (maggot) puparium fragments. These likely represent postdepositional intrusion by larvae hatched from eggs deposited on the feces by small unidentified flies.

Seeds from seven identified and two unidentified taxa were recovered in the coprolites, although in small quantities, and evidence for seed consumption is more common in EH coprolites than YD coprolites. Seeds were likely processed prior to consumption to aid in digestion; this coupled with further breakdown during digestion likely resulted in a small number of surviving seeds relative to the number of seeds ingested (Reinhard and Bryant 2008). The Paisley coprolites provide evidence for consumption of wild rose, tansy mustard, cattail, grass, amaranth, and sedge seeds and fruits. Wild rose, tansy mustard, cattail, grass, and amaranth seeds and fruits recovered from YD/EH archaeological deposits at the Paisley Caves have been previously linked to human diet (Kennedy 2018, p. 283). Our study provides direct evidence supporting previous research and offers insight that sedge seed may also have been a component of human diet during the WST occupation of the caves.

Seeds such as cattail with low MNI are interpreted to represent intentional consumption in this study. However, this needs to be further explored in forthcoming analyses of additional coprolites from this time period. Northern Paiute populations in the Great Basin harvested cattail seeds, flash burned the seeds to remove the seed fluff and toast the seeds, then winnowed and aggregated the seeds to consume in large quantities (Fowler 1986; Kelly 1932). Middle to late Holocene coprolites from the Connley Caves (5700 to 3200 cal BP) in the northern Great Basin contained more than 1000 cattail seeds per gram of coprolite (McDonough 2019), likely representing similar processing and consumption to that described in the ethnographic literature. The low frequency and lack of charring of cattail seeds in the Paisley Caves samples does not appear to represent intensive cattail seed consumption. However, seed-sized food remains can be passed gradually through the human digestive system over the course of several days to weeks after initial ingestion (Alvarez and Freedlander 1924). The small number of cattail seeds recovered might therefore be the remnants of a meal consumed several days prior to deposition of the analyzed coprolites. This example highlights the need to carefully consider cultural and biological processes when interpreting dietary inputs from macrofossil remains (Shillito et al. 2020a). The lack of evidence for charring/cooking in seeds recovered from the Paisley Caves coprolites is interesting; it may be that uncharred, intact seeds were less impacted by the digestion process and preferentially preserved, or it might reflect food processing/preparation techniques that did not expose seeds to high heat in a reduced atmosphere (e.g., Märkle and Rösch 2008).

The phytolith record provides evidence for consumption of monocot and/or dicot plant material in each coprolite analyzed for this study. This indicates that plant material—primarily leaf epidermis—was consumed with all meals. Variable phytolith density between samples suggests differences in the proportion of plant material in the diet. A high frequency of monocot morphotypes including a small number of dendritic types is linked with pollen evidence for consumption of grass in coprolite 55, suggesting consumption of grass plant material in the summer or fall after flowering when the plant was producing seed. A relatively high frequency of dicot epidermal morphotypes is linked with amaranth family seed in coprolite 98, suggesting the consumption of amaranth family leaf material. With the exception of coprolite 195, there is an

increase in phytolith density in the four youngest coprolites spanning the late YD and EH possibly linked to increased consumption of plant resources. However, this needs to be further explored with larger data sets. Consumption of leaf epidermal material is an underappreciated aspect of hunter-gatherer diet. Most research focuses on nutrients that come from meat, seeds, and underground storage organs (roots and tubers). Our study suggests that leafy greens are an important component of the YD/EH diet.

The coprolite pollen data supports with high confidence the intentional consumption of legume, buckthorn, and evening primrose plant material. Legume family taxa are entomophilous, and the high frequency, concentration, and large aggregates in coprolite 195 clearly indicate the consumption of Fabaceae flowers. Plants in the buckthorn and evening primrose families are entomophilous-pollinating, and coprolites 215 and 92, respectively, contained high frequencies of pollen types from these families indicating intentional consumption. Three of the seven seed types identified in the macrofossil sample (cattail in coprolite 242, amaranth in coprolite 215, and sedge in coprolite 242) contained corresponding pollen in high frequency, concentration, and with aggregates (in 215), providing multiproxy evidence for consumption of these taxa. The other four seed types did not have pollen frequencies corresponding with the presence of seeds, possibly explained by the manner in which these seeds were prepared.

We find support with moderate confidence for intentional consumption of pondweed, sagebrush, cattail, willow, plantain, wild buckwheat, and aster family plant material. These taxa fit some criteria for intentional consumption, but ingestion from nondietary sources cannot be ruled out. For example, Rhode and Louderback (2007) suggest that flowering heads of cattail may have been used as a fire starter during WST occupation of Bonneville Estates Rockshelter. As noted above, the botanical lens in the Paisley Caves consists primarily of sagebrush matting. Collecting these materials and bringing them into the caves may have exposed individuals to increased amounts of pollen resulting in higher than expected levels in their feces.

Taylor et al. (2019) examined pollen, plant macrofossils, bone, and hair from eleven YD/EH Paisley Caves coprolites, including subsamples of three coprolites analyzed for this study (coprolites 55, 56, and 57). Notably, there are significant differences in plant macrofossil recovery and pollen frequency/concentration in subsamples from the same coprolite, adding support to research documenting variability in dietary records from samples taken at different locations of the same coprolite (Beck et al. 2019; Martin and Sharrock 1964). Taylor et al. (2019) conclude that diets leaned toward animal resources, primarily lagomorphs but also bighorn sheep (*Ovis canadensis*) and rodent (in EH contexts), with limited evidence for consumption of plant foods and no evidence for season of occupation. Our study confirms that lagomorphs were consumed in the YD, and pushes back secure evidence for rodent consumption into the YD. We found stronger evidence in the plant macrofossil, pollen, and phytolith records for consumption of plant material. Our results demonstrate that the most complete record is derived from combined multiproxy studies. These results support previous research indicating that as many as 20 coprolites from an archaeological context need to be analyzed to capture the full range of dietary diversity (Reinhard and Bryant 1992).

Seasonality and land-use variability at the Paisley Caves

Information on the life cycle and ecological distribution for the plant and animal remains in Table 3 can be used to estimate season of occupation and the ecological zones being exploited by WST occupants of the Paisley Caves. This study assumes that plants and animals recovered from the coprolites presented here were consumed in the season that they were harvested because WST sites in the northern Great Basin provide little evidence for food storage (Smith and Barker 2017; but see Connolly and Jenkins 1999, p. 103).

Our study found that wetland resources are represented in eight of the nine samples, while dryland resources are represented in four. The animals and insects represented in the Paisley coprolites are somewhat less ecologically restricted than plant taxa. However, these data can provide some additional insight to land-use patterns. Small mammals such as rodents occur in greater density in wetlands and may have been targeted here (Simms 2008, p. 41). Hare/jackrabbit was likely hunted in the sagebrush steppe grasslands as documented in the ethnographic record (Fowler 1986). Some of the taxa identified in this study do not provide relevant information on land-use patterns; for example, grass, plantain, and buckwheat are very diverse families, and species from these taxa grow in a variety of ecological zones.

The record of plant and animal resources documented in the Paisley Caves coprolites provides preliminary evidence for site occupation focused in the summer and fall, but with some potential indications of spring and winter occupation (Fig. 18). Our study largely supports previous research suggesting that the caves were occupied in the spring or late summer/fall (Jenkins et al. 2016; Kennedy 2018). Jenkins et al. (2016) link seasonal occupation to periods of resource abundance. However, our study does not find evidence for any one resource dominating the coprolite record, as would be expected if individuals were binging on seasonally available resources (Reinhard 1993). Instead, occupants of the caves appear to have been eating a wide variety of resources.

Evidence for seasonal use suggests that the Paisley Caves was occupied on a short-term basis as part of a broader seasonal round as noted by Jenkins et al. (2016). This offers a point of contrast to studies suggesting YD/EH occupations

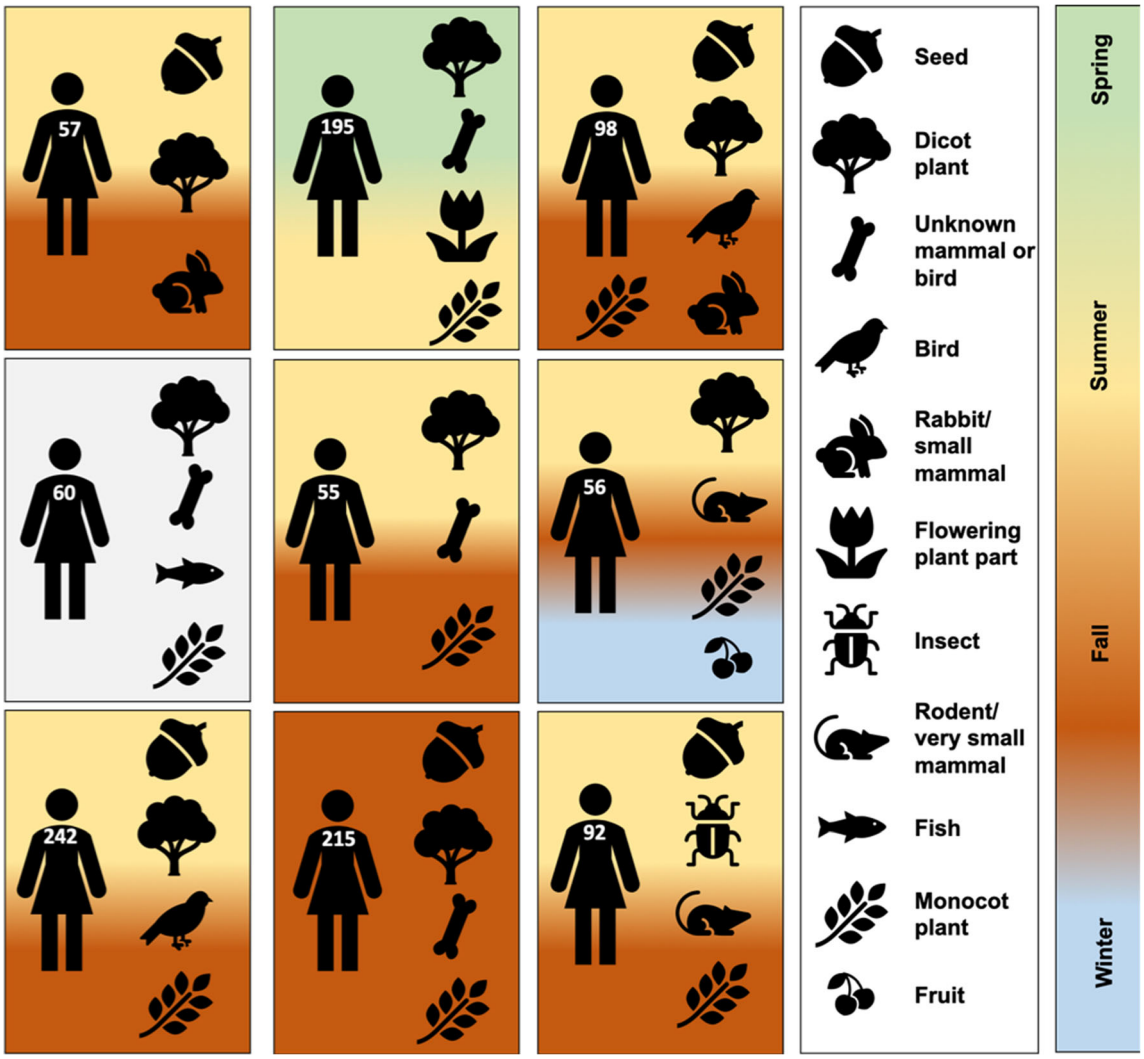

Fig. 18 Qualitative summary of dietary items with high confidence of consumption in the Paisley coprolites analyzed for this study, with estimates of likely seasonality

near wetlands were typically longer-term residential camps (e.g., Smith and Barker 2017). We present evidence for subsistence forays to a variety of ecological landscapes surrounding the caves, indicating that the wetlands below the cave likely attracted people to the Paisley Caves, but were not always the primary focus for subsistence activities. These questions of seasonality and land use are still outstanding and need to be explored further with larger data sets.

The results of this study inform on our understanding of the process of the peopling of the Americas. The WST in western North America appears to be co-eval with or may predate Clovis, so WST subsistence–settlement systems provide insight into adaptative strategies used during the spread of humans across North America. Our results indicate that YD and EH WST inhabitants of the northern Great Basin utilized a variety of local plant and small mammal resources and were not necessarily focused on large mammals for subsistence. WST inhabitants had a "settled in" seasonal subsistence strategy centered on wetland and riparian resources. This study does not present data from the earliest Bølling-Allerød WST occupations of western North America; however, our research suggests this pattern was well-established by the YD and likely reflects a similar adaptation practiced by the initial occupants of the Great Basin. This contrasts with our understanding of the initial settlement of North America described in the Clovis model, characterized by people trekking long distances across the continent following large mammal populations (Kelly and Todd 1988).

Conclusion

The multiproxy results presented in this study found strong evidence to support a diverse diet in the northern Great Basin

during the YD and EH. Western Stemmed Tradition occupants of Paisley Caves 2 and 5 clearly consumed a variety of small mammal, plant, and insect food resources. This study provides the earliest examples of whole rodent consumption and the first direct evidence for consumption of ten-lined June beetle and desert stink beetle in the northern Great Basin. Our study complements existing plant and animal data sets derived from sedimentary contexts at the Paisley Caves and adds clarity to human dietary decisions during a period with sparse direct evidence. The combined data support models proposing a broad-based subsistence strategy in the northern Great Basin during the WST and suggest that studies focused on evidence for a narrower diet breadth in terminal Pleistocene North America may be missing important subsistence diversity. Well-preserved remains at the Paisley Caves offer an opportunity to examine Pleistocene subsistence strategies in a setting that has not been impacted by issues of sampling and taphonomy that may have preferentially preserved evidence for large mammal hunting at other Pleistocene-aged sites (e.g., Cannon and Meltzer 2004, 2008).

The results of this study offer support for occupation of the caves during the summer and fall, by individuals foraging on wetland, sagebrush grassland, and riparian landscapes. The evidence supports seasonal occupation of the caves but finds that occupation may not have always been focused on harvesting resources available in abundance (c.f., Jenkins et al. 2016). Wetland food resources were important during the WST occupation of the Paisley Caves, but occupants of the caves exploited a broad range of ecological landscapes. As Jenkins et al. (2016) note, receding lake levels in the YD and EH appear to have provided a productive mosaic of ecological niches that were exploited by occupants of the Paisley Caves. This new data provisionally supports previous research indicating that Pleistocene inhabitants of western North America had a broad-based diet and wetland/riverine adaptation, potentially linked to an initial coastal migration (Davis et al. 2012; Erlandson et al. 2015; Madsen et al. 2015). Moving forward, our research will seek to explore explanations for the inclusion of seemingly low-calorie resources and the relative frequency of this type of food in a larger sample set. In doing so, we will be able to address questions of human dietary choice, specifically the role of maximizing caloric gain versus nutritional needs and cultural preferences.

Our multiproxy approach provides novel observations on diet through individual analytical techniques. These results highlight the need for multiproxy analyses to present a more robust picture of human diet (Shillito et al. 2018; Shillito et al. 2020a). Coprolites provide direct evidence of human consumption that can be used to both compliment and clarify faunal and plant material recovered from archaeological sediments. Our ongoing study will integrate these lines of evidence for a holistic view of human diet and land use throughout the sequence of human occupations at Paisley Caves.

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